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The Life Cycle and Ecology of Octospiniferoides Chandleri Bullock 1957 (Acanthocephala).

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THE LIFE CYCLE AND ECOLOGY OF *Octospiniferoides chandleri* BULLOCK 1957 (ACANTHOCEPHALA)

A Dissertation

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ABSTRACT

The life cycle of Octospiniferoides chandleri was completed experimentally in the laboratory and its population was studied over a 15-month period in a small farm pond in south Louisiana.

O. chandleri completed development to the cystacanth stage in the ostracods, Cypridopsis vidua (Müller 1776) and Physocypria pustulosa (Sharpe 1898), in 20 days at 23 C. Twenty three-day-old cystacanths were infective to mosquitofish, Gambusia affinis. Development of female worms in the definitive host took place in four distinct stages while male development was gradual. Females grew faster than males and lived longer. Duration of the earliest female stage was inversely related to temperature. Parasite transmission to the definitive host was aided by parasite-induced positive phototaxis and transfer of enteric worms through mosquitofish cannibalism.

Mature O. chandleri were found only in cyprinodontiform fishes and infection intensities were greatest in lentic habitats. O. chandleri was shown to compete with the trematode, Homalometron armatum, in mosquitofish alimentary tracts but competition had minimal effect on the distribution of O. chandleri among aquatic habitat types.

In Tramline Pond, O. chandleri was distributed among mosquitofish hosts according to the negative binomial distribution. Large fish and females were more heavily infected than small fish and males. Acanthocephalan site preference in the mosquitofish alimentary tract varied with worm size (age) and sex.

Changes in O. chandleri density suggested seasonal patterns similar to those reported previously for other acanthocephalans with

recruitment peaks in fall and winter. But, when adjustments were made to compensate for the effect of temperature upon duration of earliest juvenile stages, major recruitment was shown to take place in spring and summer. The seasonal patterns of O. chandleri and its mosquitofish host meshed well.

O. chandleri may have caused reduced fat storage in mosquitofish but had no effect upon host fecundity. There was no evidence that O. chandleri infections cause definitive host mortality and mosquitofish population regulation by this parasite was judged unlikely. O. chandleri may, however, play a part in the population regulation of its ostracod host.

INTRODUCTION

When defining animal interactions, ecology textbooks usually are careful to distinguish between parasitism and predation (Clarke, 1954; Odum, 1971; Solomon, 1971). But, when the roles of these interactions in population control mechanisms are discussed, parasites are not mentioned (Boughey, 1968; Kendeigh, 1974) or are dismissed as being functionally equivalent to predators (Browning, 1963; Colvinaux, 1973; Krebs, 1972; Solomon, 1971). To support the argument of functional equivalence between predator-prey and parasite-host systems, ecologists use examples from the vast literature on agriculturally important arthropod parasitoids. This choice of documentation is necessitated by a dearth of good quantitative studies on "true parasites" as exemplified by the endoparasitic helminths. The parasitoid literature generally supports the thesis that predators and parasitoids function similarly. But, since arthropod parasitoids occupy the "gray area" between predators and true parasites, the conclusion that all parasites are functionally equivalent to predators is suspect. If parasite-host and predator-prey systems are fundamentally different in function, a vast area of animal interactions remains essentially unexplored.

Recent evidence suggests that there are fundamental differences between predator-prey and parasite-host systems. Predators generally have a destabilizing effect upon prey populations unless special conditions such as prey refuges, invulnerable classes of prey, spatial heterogeneity, or predator switching are brought into play (Murdoch and Oaten, 1975). On the other hand, Crofton (1971b) has shown that

parasite-host systems are intrinsically stable. This stability derives from the overdispersed nature of parasite distributions in host populations that seems to be characteristic of these systems (see Crofton, 1971a, 1971b; and Pennycuik, 1971a&b).

If progress is to be made toward resolving the question of whether or not predator-prey and parasite-host systems are fundamentally different, quantitative studies of endoparasitic helminth populations of the type urged by Kennedy (1975) must be done. These should be designed to shed light upon the roles that parasites play in ecosystems. Where possible, such studies should attempt to provide evidence for judging the validity or amending schemes such as that proposed by Crofton (1971b) to explain parasite function.

The present study describes the life cycle of Octospiniferoides chandleri Bullock 1957 and its spatial and temporal (seasonal) distributions in south Louisiana. The findings of the study are discussed in terms of the possible roles of parasites in ecosystems.

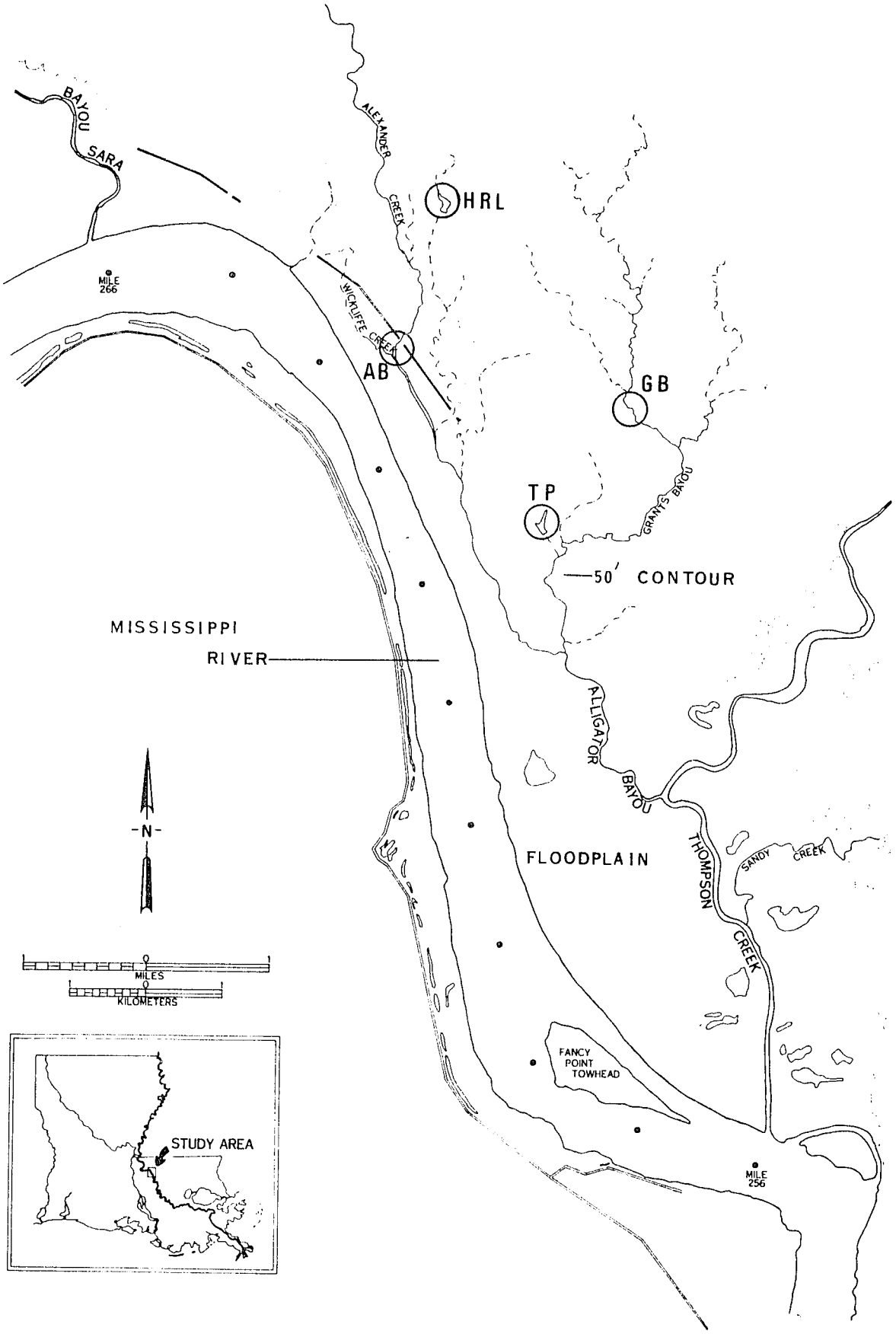
The Study Area

The principal study area was located approximately 5 km south of St. Francisville, Louisiana on land acquired by Gulf States Utilities Company to build its River Bend Nuclear Station. Initial collections in the area were part of biological studies related to power plant licensing. Most of the information in this section has been taken from the environmental report submitted by Gulf States Utilities Co. (1974).

Principal collection sites were in ponds and streams on the Alexander Creek - Alligator Bayou drainage which empties into the Mississippi River via Thompson Creek (Figure 1). Tributaries of this system in the study area arise in uplands formed by the Citronelle Terrace of late Pliocene to early Pleistocene Age. These uplands are well sculptured with good drainage and have mean elevations near 37.5 m MSL. The characteristic orange-red soils support mixed hardwood forests of sweetgum, cherrybark oak, water oak and winged elm. Former agricultural clearings are coming back in loblolly pine. Downstream, Alligator Bayou and its tributaries cut deep gullies through the younger Port Hickey Terrace which overlaps the former erosion slopes of the Citronelle. Box elder, hackberry, sweetgum and sycamore are common on these less well-drained soils. Another younger terrace discontinuously preserved along Alexander Creek is probably related to the Deweyville Terraces. Youngest upland formations are deposits of loess which blanket both the Citronelle and Port Hickey terraces. On the present floodplain of the Mississippi River, Alligator Bayou flows south towards Thompson Creek in a "Yazoo-type" channel between the backslope of the river's natural levee and the eastern valley wall formed by the terraces (Figure 1). This flat, poorly drained area supports a mixed stand of tupelogum and baldcypress.

Climate in the study area is humid subtropical. Mean summer temperatures are near 28 C with maxima near 23 C. Rainfall in summer averages about 13 cm/month. Winter temperatures have a mean near 12 C and maxima near 18 C and average rainfall is similar to that in the summer. In general, rainfall tends to be highest in the month of May and lowest in September. Temperatures generally peak in

Figure 1. Study area showing Hickory Ridge Lake (HRL), Alligator Bayou (AB), Grants Bayou (GB) and Tramline Pond (TP) collection sites. The 50 foot contour marks the eastern boundary of the Mississippi River floodplain in the area.


BAYOU SARA
ALEXANDER CREEK
HRL
MILE 266
WICKLIFFE CREEK
AB
GB
TP
GRANTS BAYOU
50' CONTOUR
MISSISSIPPI RIVER
ALLIGATOR BAYOU
THOMPSON CREEK
SANDY CREEK
FLOODPLAIN
FANCY POINT TOWHEAD
MILE 256
-N-
MILES
KILOMETERS
STUDY AREA

July and are lowest in January.

Four collection sites in the Alexander Creek - Alligator Bayou drainage were sampled during the study. Each of these constituted a distinct type of aquatic habitat.

Tramline Pond (TP in Figure 1) was the site of most concentrated effort. This man-made pond was constructed approximately 20 years before the start of the study to provide water for stock and some recreational fishing for the landowner. The elevated bed of an old tramway forms most of the shore along the southwest side while an earthen dam from the tramway to the slope of the Port Hickey Terrace forms the shore on the southeast. The northeast and northwest shores of the pond are formed by the erosion slopes of the Port Hickey Terrace. Depths in the pond range from a few centimeters in the headwaters to approximately 3 m near the dam. The surface area is approximately one hectare. Water exits the pond via a standpipe located near the dam. During long periods of drought, the pond level may drop as much as 2 m. At this level the surface area is only one half of maximum pool area and terrestrial grasses rapidly colonize the exposed slopes. These grasses, when inundated, provide food and cover for small fishes, insects and microcrustaceans. The water level fluctuations in the pond preclude the development of rooted aquatics. The northeast and northwest shores of the pond are wooded with those species mentioned earlier as being typically present on the Port Hickey Terrace. At high water the trunks of many trees in the headwaters at the northern end of the pond are inundated. Fish species present include the largemouth bass, Micropterus salmoides; bluegill, Lepomis macrochirus; green sunfish, Lepomis cyanellus; bluegill-green

sunfish hybrids, channel catfish, Ictalurus punctatus; and western mosquitofish, Gambusia affinis affinis.

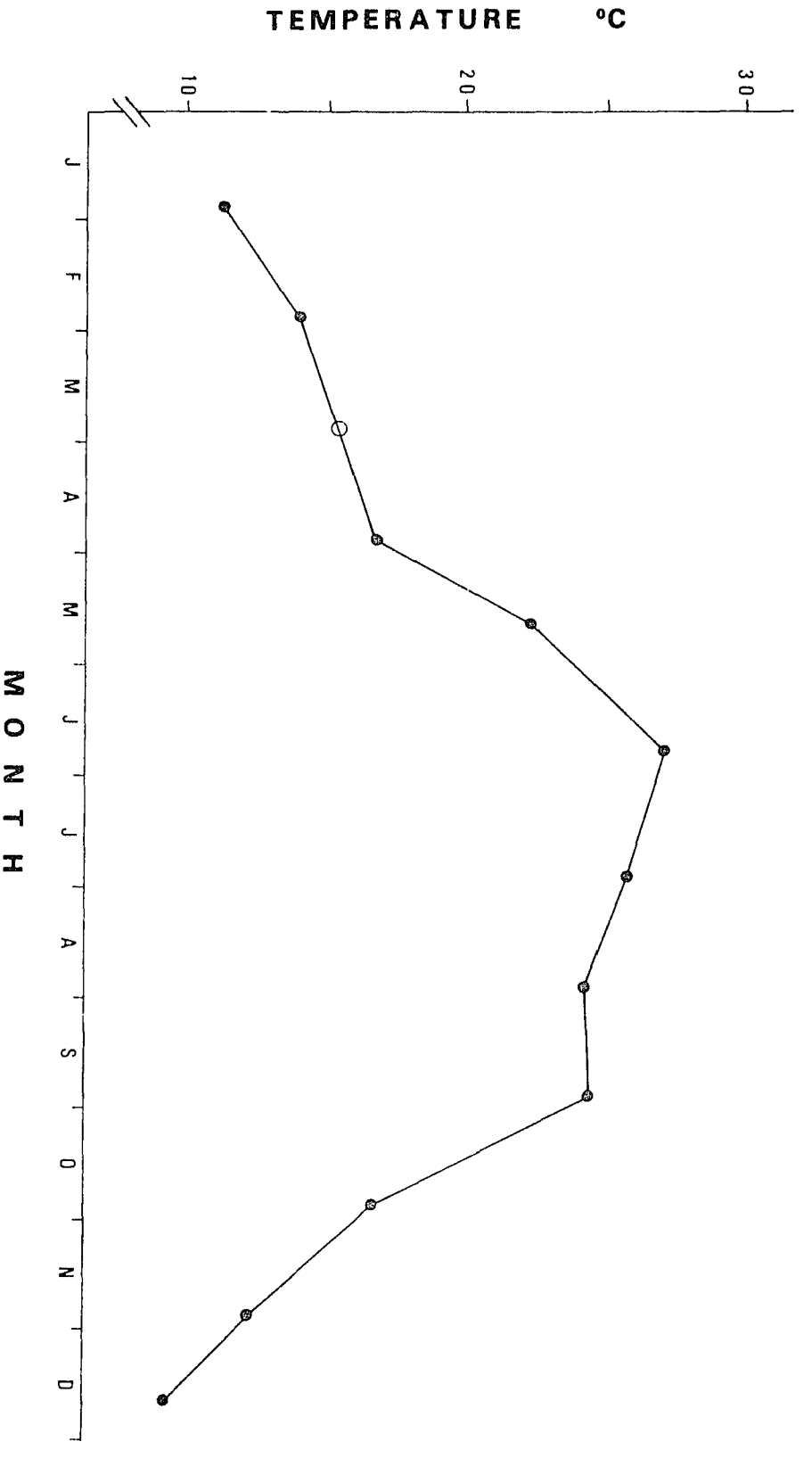
Grants Bayou is a sandy bottom intermittent creek which drains the old Mississippi River terraces and joins Alligator Bayou about 2 km above where that stream enters Thompson Creek. The total length of its drainage is 25.1 km. In the area sampled (GB in Figure 1), the stream cuts a channel 4 to 5 m deep and 10 to 20 m wide. The total drainage area above the sampling site is 24.7 km^2. Average flow in this section of the stream is about 0.3 m^3/s while floods of annual frequency may have flows as high as 87 m^3/s. Because of the relatively steep gradient of 3.15 m/km, flows return to normal 24-72 h after heavy rains. Most often, flow in the stream consists of a mere trickle 1 to 3 cm deep and 1 to 10 m wide between pools. Maximum depth in the pools during these times is near 1 m. Frequently, all flow ceases leaving the pools isolated and on rare occasions the pools have dried. The dominant substrate is coarse sand with some gravel. In some places outcroppings of clay are exposed or mud from collapsed banks is present. Throughout the collection area, the stream is protected by a forest canopy and aquatic vascular plants are absent. All fish species present in Tramline Pond were taken in Grants Bayou with the exception of Ictalurus punctatus. Twelve fish species not found in Tramline Pond were collected in Grants Bayou during the study.

Alligator Bayou is the lower section of Alexander Creek that traverses the Mississippi River floodplain and collects Wycliffe Creek and Grants Bayou before joining Thompson Creek. As Alligator Bayou's major tributary, Alexander Creek drains 62.1 km^2 of the old river terraces immediately north of the Grants Bayou drainage. This stream

is physically similar to Grants Bayou except that its greater drainage allows a greater mean flow (0.87 m^3/s) and a more consistent flow. The area in which I made collections is located entirely on the floodplain (AB in Figure 1). In the upper part of this station the stream consists of several anastomosing channels flowing across the floor of the swamp. Depths in the area are usually less than 0.3 m except where the stream scours around old tramway pilings or is dammed by beavers. In such places the stream is 1 to 2 m deep. Substrates are fine sediments and organic material above gray clay. Vegetation in this area consists of submergent beds of stonewort, Nitella sp., and water starwort, Callitriche heterophylla, and such emergents as panic grass, Panicum gymnocarpon; pickerelweed, Pontedaria sp.; and duck potato, Sagittaria sp.. The lower section of this station includes a small meander scar lake known as Grassy Lake, Needle Lake or Needle Bayou. This lake is approximately 1 km long and 10 m wide over most of its length. It is uniformly 1.5 m deep and its bottom is rather firm gray clay. The shoreline is almost completely lined with a wide belt of giant cut grass, Zizaniopsis miliacea. Water temperatures are near 10 C in January and December and exeed 25 C in June and July (Figure 2). Forty-one species of fishes have been collected in Alligator Bayou and Alexander Creek including all species present in Tramline Pond.

Hickory Ridge Lake (HRL in Figure 1) is a small lake on an unnamed tributary of Alligator Bayou that seems to have been formed originally by a beaver dam. This lake has a surface area of approximately 6 ha and is uniformly about 1.2 m deep. It is usually choked with alligator weed, Alternanthera philoxeroides.

Figure 2. Mean monthly water temperature over a three year period in the Grassy lake section of Alligator Bayou. March data (open circle) was not included because it was influenced each year by river water (C.F. Bryan and J.V. Connor, Unpublished data).


TEMPERATURE °C
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Background

Acanthocephala - General

Members of the Phylum Acanthocephala are obligate intestinal parasites of vertebrates. As their name implies, they are characterized by a spiny, retractile attachment organ or proboscis at the enterior end. Most acanthocephalans are less than 2 cm long (Crompton, 1970). The body is non-segmented, elongate, round or flattened in cross section, and is generally white.

Hyman (1951) considered the differences among the major divisions of Acanthocephala to merit only ordinal rank. Thus, the phylum has no classes and is divisible directly into three orders; Archiacanthocephala, Palaeacanthocephala and Eoacanthocephala. Archiacanthocephalans are parasites of mammals and birds and nearly all have terrestrial life cycles. Palaeacanthocephalans parasitize birds, mammals, and fishes and most have aquatic life cycles. Eoacanthocephalans are primarily parasites of fishes and all known life cycles involve aquatic first intermediate hosts.

Acanthocephalans have no digestive tracts and nutrients are obtained by direct absorbtion of partially digested food from the host intestine. The sexes are separate. Males usually have two testes arranged in tandem at mid-body. These empty to the outside via ducts and a seminal vesicle through a muscular, protrusible, copulatory sack called the bursa which is located on the posterior end of the worm. Females have a single ovary which, very early in the maturation process, splits into many ovarian balls. The ovarian balls are held in a mid-body ligament sack or float free

in the pseudocoel. An egg sorting device known as the uterine bell is connected to the posterior genital opening by a muscular uterus and a terminal vagina. Fertilization is internal. During copulation the male seizes the posterior end of the female with the extended bursa, inserts the penis, and injects sperm into the vagina. After copulation the male seals the vaginal opening with adhesive proteinaceous material from specialized cement glands. Fertilized eggs, (embryos) are released from the ovarian balls and develop in the pseudocoelom. Fully formed eggs, usually referred to as shelled embryos or shelled acanthors, are selected by the uterine bell to be passed through the uterus and vagina and released (Nicholas, 1967).

All acanthocephalan life cycles involve an arthropod intermediate host and a vertebrate final host. In terrestrial life cycles, insects usually serve as intermediate hosts while crustacea serve in aquatic life cycles. Eggs released with the feces of the definitive (final) host hatch after being ingested by a suitable arthropod. The infective stage or acanthor penetrates the midgut of the arthropod and soon develops into the acanthella stage. The acanthella stage is characterized by much growth and differentiation resulting finally in an infective larva that resembles the adult worm in every respect except sexual maturity. This larva enters a resting stage called the cystacanth. When the infected arthropod is eaten by a suitable vertebrate host, the cystacanth excysts in the alimentary tract, everts its proboscis, and attaches to the intestinal wall. Here the juvenile worm matures, mates, and the cycle is repeated.

In some acanthocephalan life cycles a third host is involved. When an unsuitable host ingests an infected arthropod or when a

suitable host ingests a worm that has not quite developed its full infectivity, the juvenile worm may burrow through the gut and encyst in the tissues of this host (De Giusti, 1949). A host infected in this way is usually referred to as a transport host although many other terms have been applied. A suitable final host may become infected by eating the transport host.

Although the investigation of acanthocephalan biology has lagged that of other helminth parasites, the last two decades have seen a rebirth of interest in this group. Acanthocephalan seasonality has recently been studied by Pennycuik (1971a), Cannon (1973), Bourque (1974), Hine and Kennedy (1974), and Amin (1975, 1977). The general acanthocephalan maturation cycle includes fall acquisition of new infections, growth and maturation in winter and spring, and egg production and death in the warm months. This simple scheme is complicated by the fact that some representatives of all stages of development are usually present in every month of the year.

The Parasite - *Octospiniferoides chandleri*

Octospiniferoides chandleri is a member of the Family Neoechinorhynchidae in the Order Eoacanthocephala. The species was described by Bullock (1957) on the basis of two immature females collected from gulf killifish, *Fundulus grandis*, near Gilchrist, Texas. Yamaguti (1963) tentatively assigned *O. chandleri* to the genus *Octospinifer*. Subsequent examination of material from the west coast of Florida indicated that the major host was the mosquitofish,

Gambusia affinis, and prompted a revised description of the worm (Bullock, 1966) which included reestablishing the genus Octospiniferoides. Schmidt and Hugghins (1974) described Octospiniferoides australis and O. incognita from South American fishes bringing the number of species in the genus to three.

The known range of O. chandleri extends from Texas around the Gulf Coast to western Florida (Bullock, 1957, and 1966). Known hosts in addition to G. affinis include: rainwater killifish, Lucania parva; least killifish, Heterandria formosa; bluefin killifish, Lucania goodei; flagfish, Jordanella floridae; gulf killifish, Fundulus grandis; and an immature shiner, Notropis sp. (Bullock, 1966).

The life cycle and ecology of O. chandleri have not been previously investigated. Life cycles that have been experimentally determined for other members of the family Neoechinorhynchidae are summarized in Table 1. All have aquatic cycles and most employ ostracods as intermediate hosts. All but Neoechinorhynchus cylindratus and N. emydis require only two hosts.

The Host - Gambusia affinis affinis

The Western Mosquitofish, Gambusia affinis affinis, is a small viviparous fish in the family Poeciliidae. Its natural range extends from the Rio Panuco in northern Veracruz, Mexico northward to southern Indiana and eastward to southern Alabama (Darnell, 1962; Rosen and Bailey, 1963). An eastern subspecies, G. a. holbrooki occurs from southern Alabama and Florida northward on the coastal

Table 1. Neoechinorhynchid acanthocephalan life cycles which have been confirmed by experimentation. Additional hosts reported by many authors have been ommitted here for clarity.

Acanthocephalan	First Host	Transport Host	Definitive Host	Authority
Neoechinorhynchus cylindratus	ostracod	bluegill	largemouth bass	Ward, 1940
Neoechinorhynchus emydis	ostracod	snail	map turtle	Hopp, 1954
Neoechinorhynchus rutili	ostracod	crayfish	salmonid fishes	Merritt and Pratt, 1964
Neoechinorhynchus saginatus	ostracod	none	creek chub	Uglem and Larson, 1969
Neoechinorhynchus cristatus	ostracod	none	suckers	Uglem, 1972
Octospinifer macilentis	ostracod	none	white sucker	Harms, 1965
Atactorhynchus verecundus	copepod	none	sheepshead minnow	Dill, 1974
Paulisentis fractus	copepod	none	creek chub	Cable and Dill, 1967

plain to southern New Jersey.

Mosquitofish tolerate a wide range of aquatic conditions and live in a great variety of habitats. Their flat heads and upturned mouths facilitate respiration at the water surface allowing them to live in water with low oxygen tension. Because of their viviparity they require no special spawning substrates and are thus free of a restriction imposed upon many other fishes (Krumholz, 1948). Mosquitofish can tolerate temperatures from 5 C to almost 38 C and salinities approaching those of oceanic waters. Although present in lotic waters, mosquitofish seem better adapted to lentic situations where they inhabit the extremely shallow water along the shore (Dees, 1962).

The mosquitofish diet includes a wide variety of animals and plants (Barnickol, 1941; Harrington and Harrington, 1961). Rice (1942) found that microcrustacea and the nymphs and larvae of aquatic insects were the most important food items of G. affinis in Reelfoot Lake, Tennessee. Efficient predation upon mosquito larvae and pupae has resulted in introductions of mosquitofish throughout the United States and to many places abroad (Krumholz, 1948). They have been successfully used to control nuisance mosquitoes (Hoy and Reed, 1970; Fisher, Smith and Enns, 1970), malaria (Holland, 1933) and even schistosomiasis (Davadie and Metge, 1965). Goodyear, Boyd and Bayers (1972) demonstrated that the voracious feeding of mosquitofish can have dramatic effects upon small ecosystems.

In keeping with its carnivorous diet, the alimentary tract of the mosquitofish is simple, short, and basically "S" shaped with only two major bends. No ceca are present. The alimentary tract is wider

anteriorly and tapers slightly toward the anus. There is no anterior sack separated from the rest of the gut by a sphincter leading many investigators to conclude that no stomach is present. But Bullock (1967) demonstrated histochemically that the anterior region of the gut performs the functions of a stomach even though it is not a distinct organ. The posterior-most 25% of the gut forms the rectum which is set off by a sphincter.

Mosquitofish breed continuously during the warm months of the year. The onset of reproductive activity in the spring is controlled primarily by temperature (Medlin, 1951). Females can store sperm which fertilizes each successive group of eggs as it develops (Breder and Rosen, 1966). Thus, one mating is sufficient to allow a female to produce young for a whole reproductive season. Females which overwinter as juveniles and mature early in the breeding season can produce four (Dulzetto, 1934, 1935; Krumholz, 1948) to six (Hildebrand, 1917) broods in a season. These fish usually do not survive the second winter but die as the oldest and largest members of the population as they approach one and one-half years of age. Females born early in the breeding season mature, produce one or two broods in that season, and then die (Krumholz, 1948). The mean period between successive broods is approximately 28 days (Breder and Rosen, 1966) and broods usually contain between thirty and forty embryos (Kuntz, 1913; Hildebrand, 1917, 1921). Brood sizes in excess of one hundred are not uncommon (Krumholz, 1948) and exceptionally large broods of 315 and 354 have been reported by Krumholz (1948) and Bonham (1946), respectively.

Although few studies have concentrated specifically on the parasites of G. affinis, many helminth parasites have been reported as a result of surveys. These reports have been conveniently summarized by Hoffman (1967) and Davis and Huffman (1975). Mosquitofish act as intermediate hosts for 25 trematodes, 5 nematodes, 2 cestodes and 3 acanthocephalans. As adults, most of these worms are parasites of birds but many are found in piscivorous fishes and mammals. Three trematodes, two nematodes, one cestode, and one acanthocephalan have been reported as using G. affinis as a final or definitive host. The single acanthocephalan using G. affinis as a definitive host is Octospiniferoides chandleri (Bullock 1966).

METHODS

Examination of Fishes

Fishes were killed by pithing. Total length, standard length, sex and general condition were noted. After external examination under the dissecting scope at 12x, the right eye of the fish was removed and examined for metacerariae.

Internal examination began with the removal of the left pectoral fin and opening the left side of the body with forceps. The visceral mass was removed and the organs examined singly at 24x. In female fishes the condition of the ovary was noted and developing embryos were counted. In both sexes, the relative development of adipose tissue in the mesenteries along the intestines was evaluated and assigned a value of zero to ten. The intestine was slit longitudinally and its contents removed and examined. All helminths were counted and their positions in the host, noted. All specimens of Octospiniferoides chandleri and representatives of other species were preserved. The presence of parasites other than helminths was noted.

Parasite specimens selected for preservation were treated as follows: Acanthocephalans were relaxed overnight in refrigerated tap water, fixed in ethanol-formalin-acetic acid fixative (AFA), and later removed to 70% ethanol for storage. Nematodes were fixed in hot 70% ethanol and stored in the same fluid. Trematodes were fixed with AFA under slight coverslip pressure and stored in 70% ethanol. Cestodes were allowed to relax in tap water, then killed in hot water, fixed in AFA, and stored in 70% ethanol. Some small cestodes and

larvae were treated as trematodes. Selected specimens were stained in Meyer's acid carmine, dehydrated, cleared in oil of wintergreen and mounted in kleermount.

Life Cycle Investigation

Ostracods (Cypridopsis vidua) were mass-cultured in the laboratory in several types of vessels. Best results were obtained using large flat containers with less than 3 cm of aged tap water. Such containers did not require aeration but at least a partial cover was required to reduce evaporation. The best and cheapest food consisted of small bits of clover and dandelion leaves crushed to a pulp between the fingers. Cultures seemed to do better if tiny amounts of raw fish flesh or cooked egg white were added occasionally.

Ostracods were infected with Octospiniferoides chandleri by allowing small cultures in petri dishes to feed on shelled acanthors removed from the bodies of mature female worms. Infected cultures were examined at frequent intervals to observe the development of the acanthocephalan larvae.

Uninfected mosquitofish used in laboratory and field experiments were either raised in the laboratory or collected from Campus Lake in Baton Rouge, Louisiana. Octospiniferoides chandleri was never found at this site in five years of collecting.

To study development in the definitive host, two methods were used to establish known-age infections in G. affinis. In the first method, uninfected fishes were infected in the laboratory by feeding them infected ostracods singly or allowing them access to infected

cultures. In the second method uninfected fishes were held in ¼ in hardware cloth cages and exposed to "natural" infections in the field. Exposure times varied from 3 to 30 days and in each case the assumption was made that the largest worms were oldest and were acquired on the first day of exposure. The smallest worm in each collection was assumed to be the youngest and acquired on the last day of exposure. Intermediate sizes were assigned to intermediate times depending upon their size distribution and assuming that worms were acquired at a constant rate throughout the exposure period. Males and females were treated separately because of size and growth rate differences.

To examine the effect of temperature upon the development rate of female worms, laboratory infected mosquitofish were incubated at 23 C and 30 C and representatives were examined daily.

The possibility of fish-to-fish transfer of enteric O. chandleri through definitive host cannibalism was tested in two experiments. First, sections of intestine from infected fishes were fed to medium-sized uninfected mosquitofish. Later, small, live fish from an infected source were held in tanks free of ostracods with large uninfected mosquitofish.

The effect of larval acanthocephalans upon ostracod behavior was tested in the field by collecting ostracod samples from both surface waters and bottom waters with a #60 mesh geological sieve. These samples were examined separately for acanthocephalan infections. Further tests were conducted in the laboratory with the aid of a four-chambered plastic petri dish modified to allow ostracods to choose between a light chamber and a dark chamber. All surfaces of

the top and bottom of the petri dish were painted flat black except for a clear window on one half of the cover. Two of the four radial partitions in the bottom of the dish were breached to create two compartments. With the cover in place, and a light suspended above the dish, each compartment had a lighted and a dark chamber. Uninfected ostracods were placed in one compartment and infected ostracods in the other. The light was turned on for ten minutes and then the ostracods in each chamber were counted. After counting the cover was rotated 180 degrees to switch dark and light chambers, left another ten minutes and the procedure repeated. Results of several runs were analyzed by X^2 testing.

Competition between O. chandleri and the trematode, Homalometron armatum, was examined by experimentally establishing concurrent infections in previously uninfected mosquitofish. In the field, fish were exposed to infections in cages in concurrent, reciprocal experiments. Two groups of 60 fish each were simultaneously exposed to either the trematode (in a stream) or the acanthocephalan (in a pond) for one week. After the initial exposures, 20 fish from each group were brought to the laboratory and held as controls. The remainder in each group was superinfected by exposure to the other parasite for one week and then held in the laboratory for another week to allow interaction between the parasites. At the end of the interaction period, the two control and two treatment groups were sacrificed and all worms were identified and counted.

Seasonal Dynamics

Mosquitofish were collected by dipnet monthly from Tramline

Pond, Grants Bayou, and Alligator Bayou, over a 13 month period. Sporadic collections of mosquitofish and other hosts were made from many habitats in southern Louisiana. Approximately 20 fish from each collection were returned live to the laboratory for necropsy. At least ten of the fish from each collection were necropsied as soon as possible after capture. This was usually accomplished by the second day. Worms from these collections were preserved as described above. After preservation, they were measured (total length - including proboscis but excluding the bursa of males), sexed, female ovarian balls were counted and the presence of fertilization caps, everted bursae, round or elongate embryos was noted. Part of each collection of hosts was preserved in the field to provide additional specimens for examination. Data from these specimens were used in calculating incidence and density of O. chandleri and in determining size frequency, reproductive condition, and fat storage in mosquitofish. Worms collected by this method were not suitable for determining parasite population characteristics and were excluded from all analysis except counts.

Data Treatment

Monthly density estimates of O. chandleri populations in Tramline Pond were calculated using the following formula:

$$D_i = N_i/n_i,$$

where D_i is the mean intensity of infection (density) for month i, N_i is the number of worms recovered in month i, and n_i is the number of hosts examined in month i.

Monthly recruitment rate (R_i) was estimated using the following equation:

$$R_i = 2\ f_i/(n_i\ d_t),$$

where f_i is the number of stage I females recovered in month i, n_i is the number of hosts examined in month i and d_t is the duration of female stage I in days at mean monthly temperature t.

Use of this expression to calculate recruitment produces an estimate representative of the period of time immediately preceeding the sample date and having a duration of d_t. The method adjusts the recruitment estimate to account for the acquisition of males by assuming a sex ratio of 1:1 and doubling female recruitment.

Monthly mortality rates (M_i) were estimated from the expression:

$$M_i = (R_i + R_j/2) - \Delta D,$$

where M_i is the mortality in month i and the other variables are defined above. The mean of adjacent recruitment estimates (R_i &R_j) is used to bring the points in time best represented by ΔD and recruitment into coincidence.

Standard statistical analyses and tests contained in SAS subroutines (Barr, Goodnight, Sall and Helwig, 1976) were used for most analyses. Because acanthocephalan parasites are distributed non-normally, tests using worm counts or statistics derived from them were performed on data normalized by the square root transformation as well as on untransformed data. In no cases did data transformation alter the outcome of statistical tests.

O. chandleri distributions were fitted to the negative binomial distribution using a Fortran IV program employing the methods of

Bliss and Fisher (1953). Goodness of fit and differences between distributions were tested using the Kolmogorov-Smirnov one- and two-sample tests, respectively (Siegel, 1956).

All measurements in the text are in microns unless stated otherwise.

RESULTS AND DISCUSSION

Life Cycle and Development

Octospiniferoides chandleri completed larval development in two species of ostracods and developed to maturity in the mosquitofish *Gambusia affinis*. Two mechanisms improved the likelihood of parasite transfer between hosts.

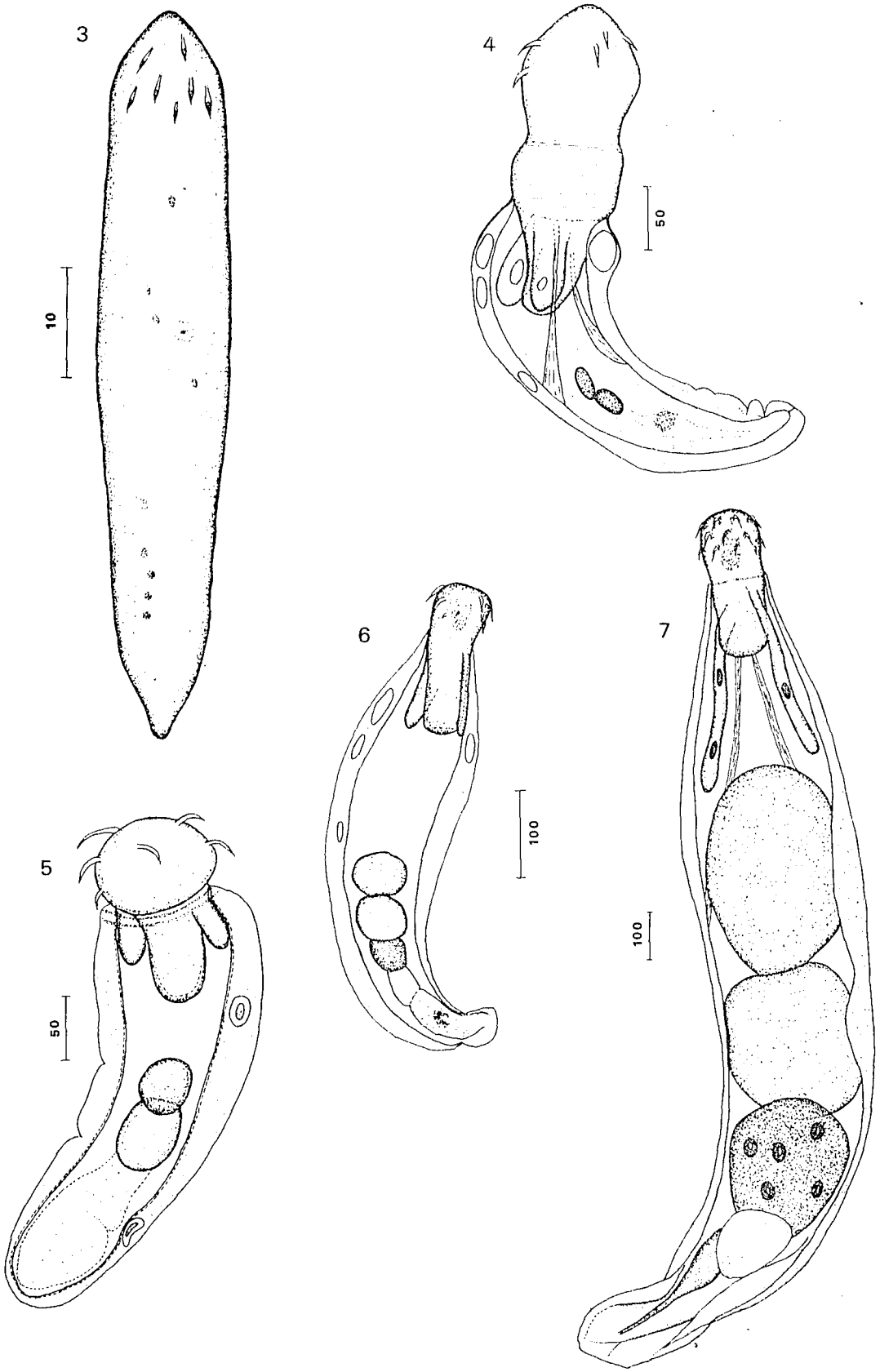
Development in Ostracod Host

In the laboratory, experimental completion of the life cycle was accomplished using both *Cypridopsis vidua* (Müller, 1776) and *Physocypria pustulosa* (Sharpe, 1898) as intermediate hosts. *C. vidua* was used in most experimental infections, however, since it proved to be much easier to culture.

Acanthor

Acanthors were studied alive and unstained after mechanical hatching on microscope slides. No movement was seen in any of the several acanthors hatched on slides. Upon hatching, the acanthor immediately increases in size from 51 by 6 to 60 by 11 (Figure 3). Increase in size has been reported for other acanthocephalan acanthors (Schmidt and Olsen, 1964; Merritt and Pratt, 1964; Ward, 1940). Nine spines arranged in diagonal rows can be seen at the anterior end. Fine body spines such as reported for *Paulisentis fractus* (Cable and Dill, 1967) are absent. The entoblast, representing the primordia of most adult organs, is elongate and so diffuse as to be difficult

Figure 3-7. Development of Octospiniferoides chandleri males. 3. Acanthor hatched mechanically under coverslip. 4. Late male acanthella from wild infection. 5. Fifteen-day-old male acanthella. 6. Male cystacanth or early juvenile. 7. Mature male.


3
10
4
50
5
50
6
100
7
100

to recognize. There is no vacular space surrounding the central nuclear mass as has been reported for Neoechinorhynchus cylindratus (Ward, 1940) and Neoechinorhynchus emydis (Hopp, 1954). Merritt and Pratt (1964) found that such spaces occurred in only a few of the Neoechinorhynchus rutili acanthors that they examined. Uglem and Larson (1969) determined that these spaces resulted from examining acanthors in hypotonic solutions.

O. chandleri acanthors most closely resemble those of Octospinifer macilentis described by Harms (1965) except that they are much more elongate and have stouter anterior spines. This is the sixth neoechinorhynchid acanthor reported to have spines on the anterior end. Only Neoechinorhynchus cylindratus and N. rutili have been reported as having anechinate acanthors (Ward, 1940; Merritt and Pratt, 1964).

Acanthella

Early acanthella stages were not observed. At 14 days post infection, the worms are clearly in the late acanthella stage. The proboscis is fully formed but is not yet withdrawn (Figure 5). Proboscis hooks are well developed and protude through the integument. Males have small but fully formed testes but their cement glands, cement reservoir, Saeftigen's pouch and seminal vesicle are not well differentiated. The acanthellae studied were 360 long and 120 wide at their greatest width. Except for being slightly smaller and much less elongate, they closely resembled Octospinifer macilentis acanthellae described and figured by Harms (1965). Unfortunately, no females were observed at this stage.

Cystacanth

By the 20th day, all larval O. chandleri examined had withdrawn their probosces and entered the cystacanth stage. There was no evidence of a cyst. Males at this stage are 360 to 490 long with the proboscis withdrawn and 400 to 550 long with it everted. Females are slightly longer measuring 400 to 540 with the proboscis in and 450 to 600 with it extended. The vast majority of both sexes evert their probosces during overnight refrigeration. Most males also evert a small but well-formed bursa. With probosces everted, both male and female cystacanths are identical to the earliest juvenile stages found in mosquitofish. Females all contain one round ovary at midbody (Figure 8a) and all adult structures are present. In males, small but distinct testes and cement glands occupy the posterior one-third of the worm. Starved, uninfected mosquitofish became infected by eating ostracods which contained 23-day-old cystacanths.

Development in Fish Host

Male Development

In the mosquitofish host, male O. chandleri development was characterized by an increase in the relative size of the testes and cement gland and slight refinement in the structure of the bursa. Also, the cement gland became progressively darker as male worms aged. All changes in development from the youngest (Figure 6) to the most mature male worm (Figure 7) were gradual. Since there were no abrupt changes, it was not possible to assign stages to male development. The age at which males reach functional maturity was not determined.

Figure 8-11. Development of Octospiniferoides chandleri females. 8a. Female cystacanth or earliest Stage I juvenile. 8b. Older Stage I female. 8c. Earliest Stage II female. 9a. Stage II condition. 9b. Post-fertilization "milky condition" with perfectly formed cement cap in place. 9c-e. Degeneration of the cement cap. 10. Development of the shelled embryo. 11. Stage IV female.

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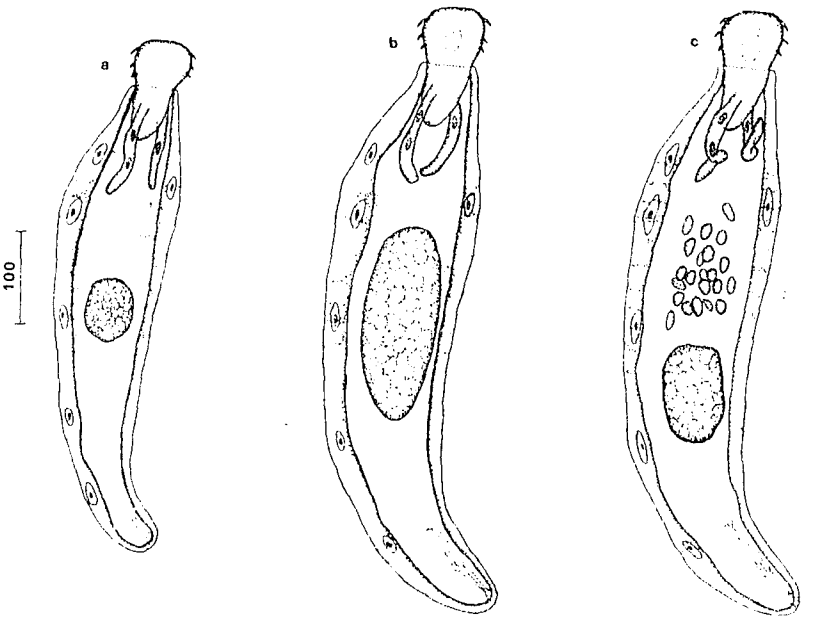

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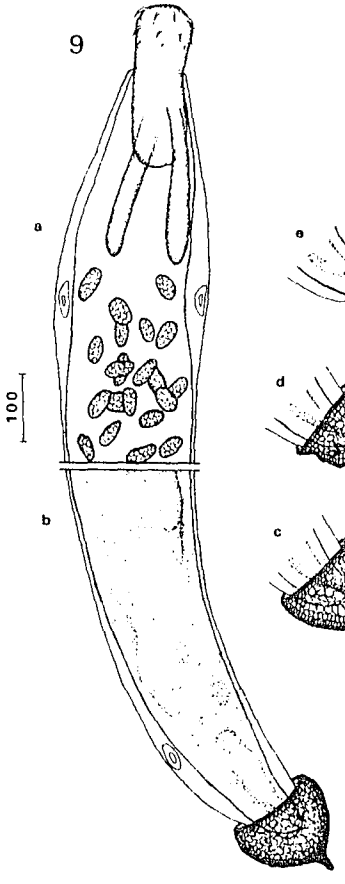

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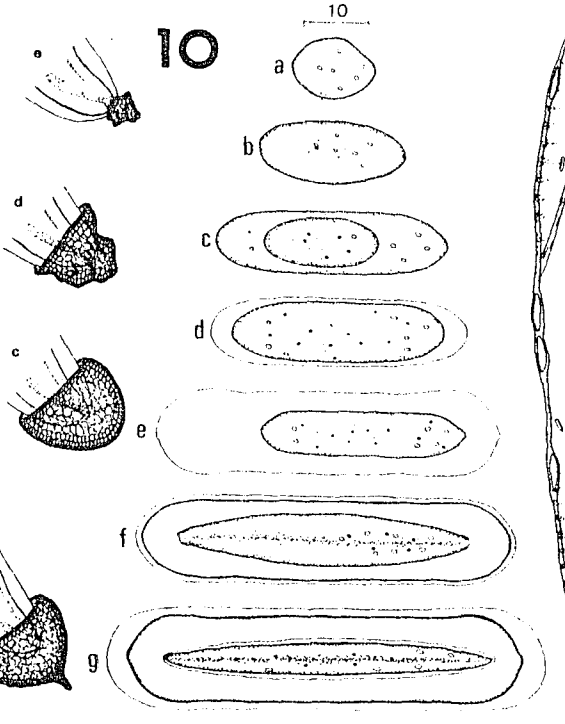

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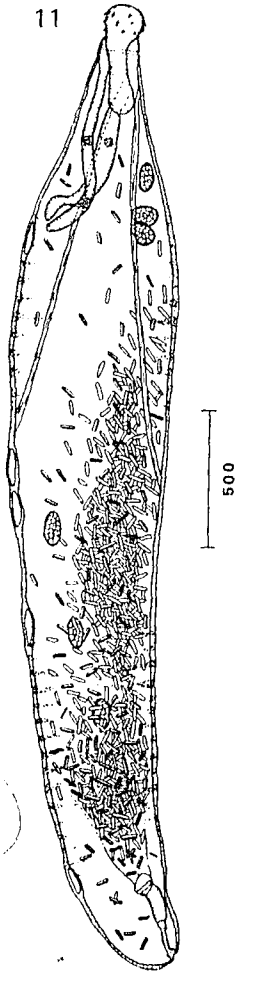


Female Development

Female O. chandleri development in the Gambusia affinis alimentary tract was found to be divisible into four distinct stages.

Stage I

Newly acquired female worms are identical to female cystacanths removed from ostracods. All have a single round or oval ovary at approximately the center of the worm body (Figure 8a). As the worm grows, the ovary elongates. The size of the ovary tends to be quite variable, but in 61 specimens in which the ovaries were measured, there was a significant linear relationship between the size of the ovary and the total length of the worm ($P < 0.0001$). The least squares regression expression for the relationship was: $L_O=0.21L_W - 60.3$, where L_O=ovary length and L_W=worm length. All female worms containing a single ovary were designated Stage I females. These were usually less than 1000 in total length (Figure 12).

Stage II

After a period of elongation, the ovary divides into anterior and posterior segments and then, almost simultaneously, each segment splits into 12 to 24 ovarian balls (Figure 8). Females with more than one ovary or ovarian ball are designated Stage II females (Figures 8c and 9a). Ovarian ball number increases linearly with increase in Stage II female length ($P < 0.0001$) but the regression expression has little value because of the extreme variability in ovarian ball numbers ($r^2 = 0.205$). Ovarian balls continue to divide until there are between 40 and 60.

Cement caps on known-age worms indicated that Stage II females

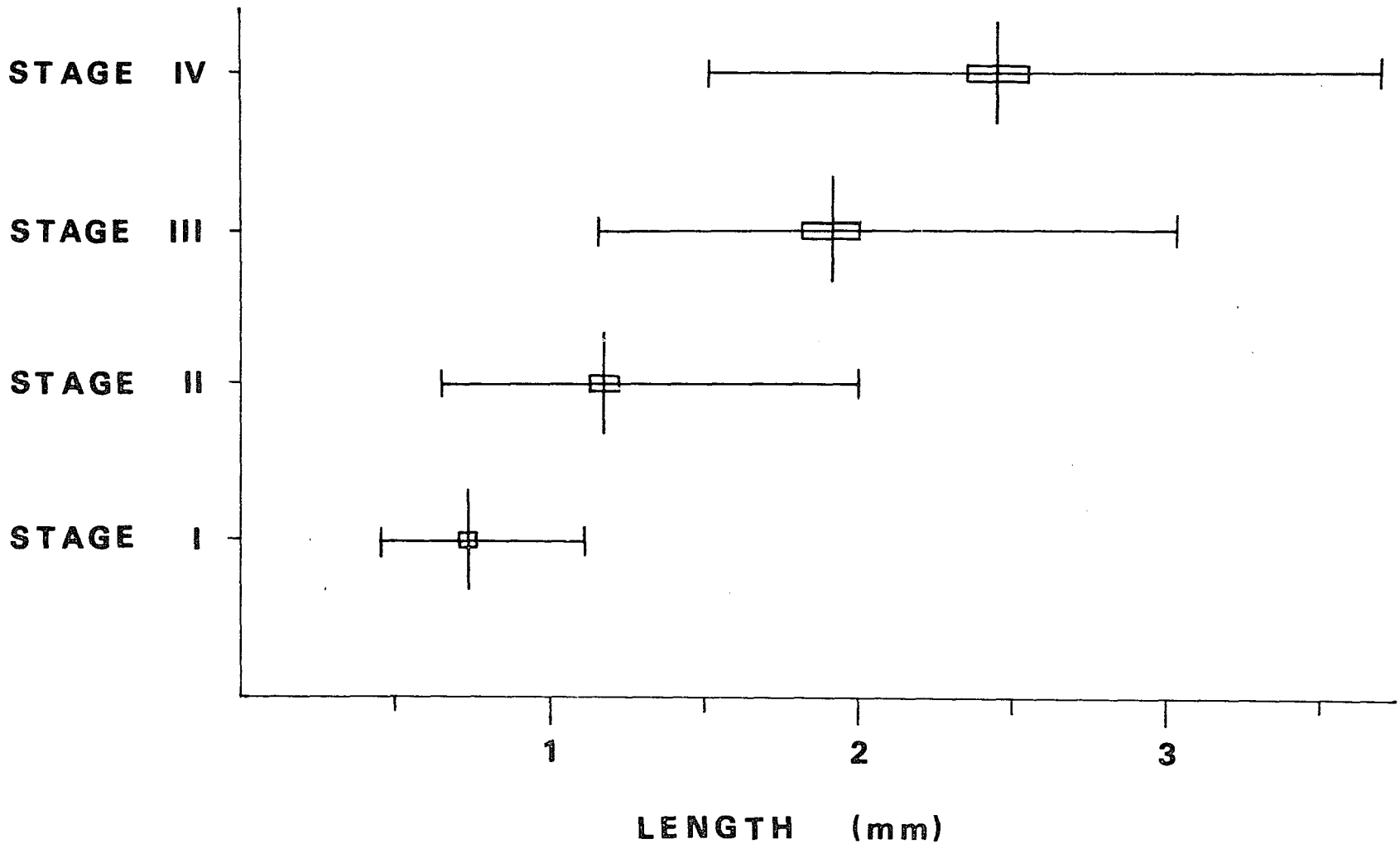
copulate when they are 17 to 33 days old (post infection) and 1050 to 1510 in length. The presence of sperm in the female pseudocoel is indicated by a "milky" appearance that obscures the ovarian balls and makes them difficult to count (Figure 9b). This condition persists after the ephemeral cement caps have degenerated and disappeared (Figure 9c-e). Thirty five "milky" females collected during monthly sampling were 790 to 1920 long (mean = 1242). Although the range is greater, these sizes compare with observations reported above for known-age worms. Both observations indicate a mean size at copulation of approximately 1250 for Stage II female O. chandleri. This is slightly above the mean for all Stage II females encountered in natural infections (Figure 12).

Stage III

As soon as developing embryos can be seen free in the pseudocoel, female O. chandleri are considered to be in Stage III of development. At this stage, the "milky" condition no longer exists and the ovarian balls can again be counted through the body wall of the female worm. The developing embryos are round, oval, or slightly pyriform in shape and some rod-shaped shelled acanthors may be present in the later portion of this stage.

The developmental sequence of the embryo in the Stage III Female is shown in Figure 10. Round embryos newly separated from ovarian balls elongate as they grow. Simultaneously, the entoblast becomes visable in the center of each embryo (Figure 10c). At its greatest size, the embryo forms an enclosing membrane from which it subsequently shrinks (Figure 10d-e). In a second phase of elongation, the embryo

Figure 12. Relationship between size and maturation stage in Octospiniferoides chandleri females. The long horizontal lines represent the range of sizes for each stage while the central vertical line and the width of the rectangle surrounding it represent the mean and standard error of the mean, respectively.


STAGE IV
STAGE III
STAGE II
STAGE I
1
2
3
LENGTH (mm)

attains its final spindle shape while the enclosing membrane differentiates into two distinct shell layers (Figure 10f-g). The fully developed acanthor is surrounded by four membranes. Observations made during mechanical hatching on microscope slides indicate that the outermost membrane is very thin and flexible. The next membrane toward the acanthor is thicker, highly refractile and rigid. This membrane appears to provide the structural support to the shell. The third membrane is the thickest of the four but is soft and flexible. The fourth membrane is very thin and forms a flexible envelope closely adherent to the acanthor.

Neoechinorhynchus saginatus was the first neoechinorhynchid acanthocephalan reported as having four membranes surrounding the acanthor (Uglem and Larson, 1969). Later, Uglem (1972) found four membranes in N. cristatus. O. chandleri is the third neoechinorhynchid acanthocephalan found to have more than the three membranes previously thought to be characteristic of the Eoacanthocephala.

Stage IV

When the proportion of rod-shaped shelled acanthors among the developing embryos exceeds 50%, the female worm is considered to be in Stage IV of development (Figure 11). Although the distinction between Stage III and Stage IV female O. chandleri requires a much more subjective decision than was used in distinguishing earlier stages, few problems arise in practice. Once the embryos begin to mature, the process seems to proceed rapidly; fully-formed shelled acanthors are predominant in the pseudocoel within a short time. Few specimens are encountered which do not clearly fall into one or the other category.

Growth

The growth rates of male and female O. chandleri in mosquitofish hosts were determined by plotting the size of known-age worms against their ages. The resulting growth curves were linear for both males ($P < 0.0001$, $r^2 = 0.94$) and females ($P < 0.0001$, $r^2 = 0.91$) (Figure 13). Females were larger than males of equal age and grew faster. The regression expression indicates that females enter the population in the fish host at a mean length of 510 and grow at a mean rate of 34/day. The largest female collected during the study was 3.7 mm long. The regression expression for males indicates that they enter the population in the fish host at a mean length of 460 and grow at a mean rate of 20/day. The largest male O. chandleri collected during the study was 1.87 mm long.

Experimentally infected mosquitofish were held at 23 C and 30 C to determine the effects of temperature upon the duration of Stage I females. At 23 C O. chandleri females required 7 days to develop to Stage II. At 30 C this process took only three days. With only two data points, the relationship between temperature and the duration of the Stage I form must be interpreted as linear even though a sigmoid relationship would be expected. The linear approximation of the relationship is reasonable since such relationships tend to be linear except where the temperature approaches the limits of tolerance of the organism. Extrapolation of the resultant curve allows estimates of the duration of the Stage I female at temperatures lower than those tested (Figure 14). Extrapolation toward the lower temperatures is believed to be conservative because the expected sigmoid relationship would cause duration times to increase faster

Figure 13. Growth rates of female (open circles) and male (dots) Octospiniferoides chandleri. The lines were fitted using the least squares method.

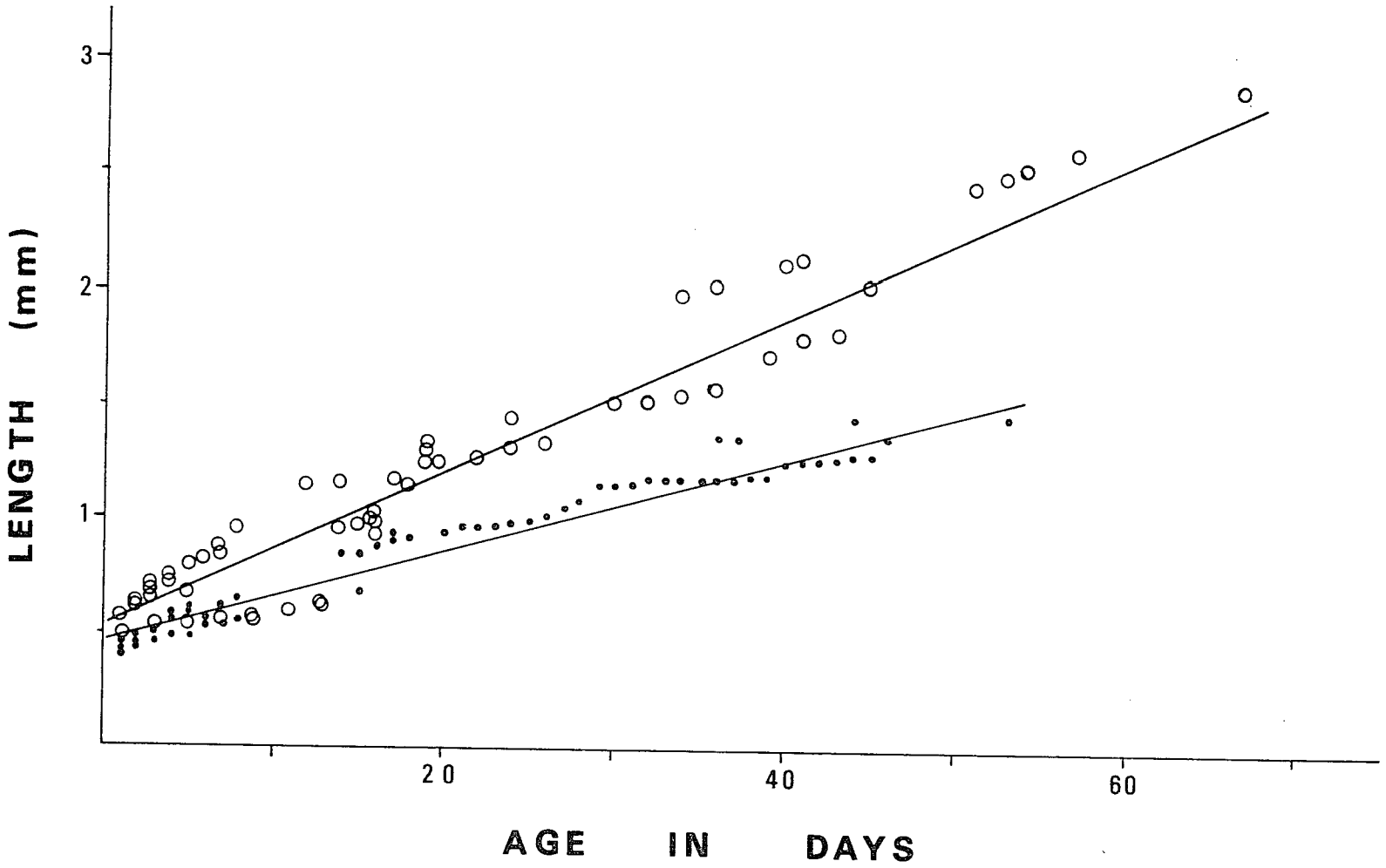
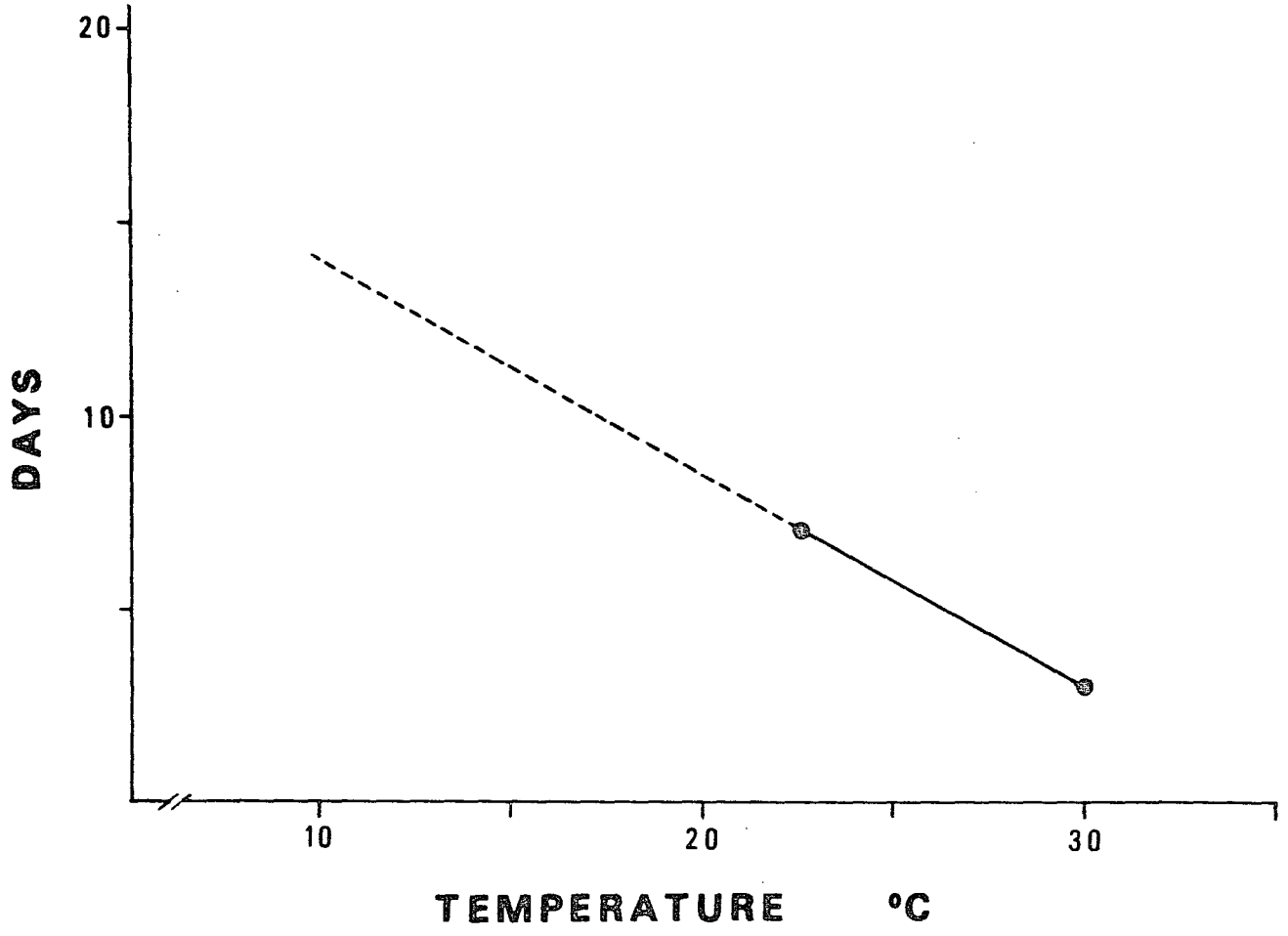

LENGTH (mm)
3
2
1
20
40
60
AGE IN DAYS

Figure 14. Relationship between the duration in days of the female Stage I condition and ambient temperature.


20
10
DAYS
10
20
30
TEMPERATURE °C

than the linear model predicts. This information has application in the determination of recruitment into the population of juvenile and adult worms to be discussed later.

Natural Transfer of Infections

Natural Ostracod Infections

In ostracod collections from Tramline Pond taken in August, September and October of 1975, six (0.8%) of 711 Cypridopsis vidua were found naturally infected with O. chandleri. In addition, 550 specimens of the ostracod Physocypria pustulosa were examined and 16 (2.9%) of these contained O. chandleri cystacanths (Table 2). No other ostracod species was collected. Cystacanths of Neoechinorhynchus cylindratus were present in 74 (15.5%) of the P. pustulosa examined. N. cylindratus is found as an adult in the intestine of largemouth bass (Micropterus salmoides) and utilizes the bluegill (Lepomis macrochirus) as an intermediate host (Ward, 1940). N. cylindratus cystacanths were readily distinguished from O. chandleri cystacanths on the basis of the large size and large proboscis hooks of the former. No C. vidua were found infected with the bass acanthocephalan. None of the naturally infected ostracods examined contained more than one cystacanth.

Both O. chandleri and N. cylindratus infections in Tramline Pond ostracods were higher than most published reports for neoechinorhynchid acanthocephalans. Ward (1940), Hopp (1954), and Harms (1965) all reported natural ostracod infections of less than 1%. Merritt and Pratt (1964) found an exceptionally high incidence (24%) among ostracods infected with Neoechinorhynchus rutili.

Table 2. Incidence of Octospiniferoides chandleri and Neoechinorhynchus cylindratus infection in the ostracods Cypridopsis vidua and Physocypria pustulosa collected at two levels in Tramline Pond, summer and fall, 1975.

	Percent Infected			
	Cypridopsis vidua (711)*		Physocypria pustulosa (550)*	
Sample Level	O. chandleri	N. cylindratus	O. chandleri	N. cylindratus
Top	2.0	0.0	6.7	38.5
Bottom	0.4	0.0	1.1	1.3
Levels Combined	0.8	0.0	2.9	13.5

*Number examined

The high incidences of infection in P. pustulosa suggest that it is the major intermediate host of both N. cylindratus and O. chandleri in Tramline Pond. In the case of O. chandleri, laboratory observations also support this conclusion. During experimental infections, starved mosquitofish readily consumed infected P. pustulosa but refused the larger, hard-shelled C. vidua until the valves were cracked slightly by squeezing them with forceps. Although a suitable host for O. chandleri in the laboratory, C. vidua probably plays a minor role in the parasite life cycle in nature.

Altered Ostracod Behavior

Ostracods infected with fully formed cystacanths exhibited behavioral patterns that are markedly different from those of uninfected animals. In laboratory cultures exposed to infection, ostracods form aggregations milling about at the surface of the water. In uninfected cultures, most ostracods are concentrated in the bottom of the jars with relatively few individuals moving about in the upper regions of the water column. Since cystacanth infections have been shown to produce a "surface-seeking" reaction in amphipods (Holmes and Bethel, 1972), I suspected that O. chandleri infections might be responsible for the strange behavior of the ostracods in the culture jars. When samples of ten ostracods each were pipetted from the surface and bottom of an infected culture jar, all of the ostracods from the surface were found to carry cystacanths and three contained double infections. In the bottom sample, only three of the ostracods were infected and all were single infections. The four-fold increase in infection intensity from the bottom to the top

of the culture jar suggests strongly that the acanthocephalan was responsible for the altered behavior of its host.

To examine the effect of natural O. chandleri infections upon intermediate host behavior, ostracod collections were taken from both the surface and bottom of the water column in the Tramline Pond littoral zone with a #60-mesh sieve. O. chandleri cystacanths were found in 2% of the C. vidua from top samples but in only 0.4% of the samples collected from the bottom (Table 2). Similarly, it infected 6.7% of the P. pustulosa collected at the surface of the water and only 1.1% of those collected from the bottom. Neoechinorhynchus cylindratus cystacanths in P. pustulosa were even more concentrated in the surface collections where they infected 38.5% of the ostracods. Only 1.3% were infected in bottom collections. In all cases the top versus bottom comparisons in Table 3 were significantly different when tested as binomial variates ($P < 0.05$). It is clear from these data that the surface-seeking behavior of the ostracods is related to the cystacanth infections.

The nature of the altered ostracod behavior was examined in the laboratory with infected and non-infected animals using a light-dark choice chamber. During the course of the five trials of the experiment 57.5% of the infected ostracods were found in the lighted chamber while only 37.8% of the uninfected controls were found in the light. The distribution of the infected ostracods over the five trials was determined by X^2 test to be significantly different from that of the controls ($P < 0.05$).

These tests suggest that the surface-seeking behavior of infected ostracods is due at least in part to a photophilic response

related to the presence of the larval acanthocephalan. An altered geotactic response might also be involved but this aspect was not investigated. Bethel and Holmes (1973) found that the surface-seeking response in amphipods infected with Polymorphus paradoxus and Corynosoma constrictum was due to an altered phototactic response with geotaxis having no measurable effect.

Regardless of the exact nature of altered ostracod behavior, it is clear that their surface-seeking response puts them in a position of optimum availability to the final host (in the case of O. chandleri) or the transport host (in the case of N. cylindratus). Similar cases of parasite-induced changes in intermediate host behavior are increasingly being documented (Holmes and Bethel, 1972). They are important because they affect the dynamics of the predator-prey relationship between intermediate and definitive hosts as well as the dynamics of parasite-host systems.

Transfer of Enteric Infections

The transfer of enteric parasites from prey to predator is often invoked to explain "accidental" infections where adult helminths occur in unusual hosts. The role of this mechanism as a normal extension of helminth life cycles has received little attention. When, as in the case of mosquitofish, the definitive host is cannibalistic, this mechanism could account for a significant amount of parasite transfer. The question of whether or not transfer of enteric parasites operates in the O. chandleri - mosquitofish system was explored in two separate experiments.

In the first experiment, six uninfected mosquitofish were

offered live adult and juvenile O. chandleri singly and in sections of alimentary tract from infected fish. Test fish were not observed to eat any of this material, but one week later one of the six fish was found to contain a single female O. chandleri 1.1 mm long. The other five fish were not infected.

In the second experiment, 39 very small mosquitofish from an infected source were offered as live food to 14 large uninfected mosquitofish. To encourage cannibalism, the large fish were given no other food. When the large fish were necropsied after one week, three were found infected with a total of seven O. chandleri ranging in size from 0.9-1.2 mm.

Results of these experiments indicate that transfer of enteric O. chandleri from small to larger mosquitofish is possible and might be expected to occur in nature. The efficiency of this method of transfer can not be determined because the number of worms in the infective material and the consumption of this material are not known. Similar transfer of enteric parasites has been demonstrated for Echinorhynchus salmonis and Moniliformis dubius (Hnath, 1969; Moore, 1946).

Summary of Life Cycle

Octospiniferoides chandleri completes larval development in an ostracod intermediate host and develops to maturity in a fish definitive host. In Tramline Pond, shelled acanthors pass with mosquitofish feces and are eaten by the ostracods, Cypridopsis vidua and Physocypria pustulosa. Larval development in the ostracod host pro-

duces cystacanths by the 20th day and these are infective to mosquitofish by the 23rd day at 23 C. Male O. chandleri development in the definitive host is gradual and direct while female development can be divided into four stages. Female worms are larger than males and grow faster. Developmental rates are determined by ambient temperature. Transmission of infections is enhanced by parasite-induced "surface-seeking" behavior in the ostracod host and transfer of enteric parasites from small to large mosquitofish through cannibalism.

Spatial Distributions

Distributions Among Habitats and Host Species

Octospiniferoides chandleri was found to infect fishes in all aquatic habitats examined in the Alligator Bayou drainage system, but mean densities (infection intensities) greater than one worm per host were found only in the lentic environments of Hickory Ridge Lake and Tramline Pond (Table 3). The highest density of O. chandleri (7.7/host) was found in mosquitofish in Tramline Pond while highest incidence (100%) occurred in Fundulus olivaceus in Hickory Ridge Lake.

Although the Alligator Bayou drainage has a rich ichthyofauna (Bryan, Conner & DeMont, 1974) O. chandleri was found to infect only one poeciliid (Gambusia affinis), two cyprinodontids (Fundulus chrysotus and Fundulus olivaceous), and two centrarchids (Lepomis macrochirus and Elassoma zonatum). Among these, only the cyprinodontiform fishes seem to be suitable definitive hosts. All cyprinodontiforms

Table 3. Distribution of *Octospiniferoides chandleri* among fishes in the Alligator Bayou drainage. Incidence is reported as percent. Intensity is the number of worms per host.

Location and Host	Number Examined	Incidence	Intensity
TRAMLINE POND			
Gambusia affinis	288	87.2	7.70
Lepomis macrochirus	36	2.8	0.03
Others (3 species)	18	0.0	0.00
ALLIGATOR BAYOU			
Gambusia affinis	183	11.5	0.30
Fundulus olivaceus	14	14.3	0.21
Elassoma zonatum	12	8.3	0.17
Fundulus chrysotus	5	0.0	0.00
Poecilia latipinna	3	0.0	0.00
Others (33 species)	176	0.0	0.00
GRANTS BAYOU			
Gambusia affinis	134	17.9	0.28
Fundulus olivaceus	14	7.1	0.07
Others (11 species)	73	0.0	0.00
HICKORY RIDGE LAKE			
Fundulus olivaceus	3	100.0	3.00
Gambusia affinis	5	60.0	1.80
Fundulus chrysotus	10	20.0	0.20

had relatively high infection rates in at least one environment or contained mature O. chandleri. On the other hand, the infections found in the centrarchids seem to be accidental. Only one worm was recovered from L. macrochirus and two from one E. zonatum specimen. These worms were immature and the specimen from L. macrochirus was very small, located in the rectum, and in poor condition. It is unlikely that either of these species is a suitable definitive host for O. chandleri.

The data in Table 3 seems to indicate that the mosquitofish is the major definitive host for O. chandleri among the suitable hosts in the drainage. Density was highest in mosquitofish for every habitat except Hickory Ridge Lake and the number of hosts examined there makes those data suspect. The mosquitofish tends to be the numerically dominant form in most habitats. Even if infection densities were equal between it and another species such as F. olivaceus, mosquitofish would still carry most of the O. chandleri population. This numerical dominance is especially pronounced in the more lentic habitats where O. chandleri infections seem to concentrate. Bullock (1966) found the mosquitofish to be the major host of O. chandleri in Florida where highest infection rates occurred in lentic habitats. In southern Louisiana habitats examined outside of the Alligator Bayou drainage, O. chandleri infections in mosquitofish were again found much more frequently in lentic situations than in lotic situations (Table 4). Infections were found in the Comite River near Greenwell Springs Road but both incidence and intensity were low. Infections were not present in all lentic habitats. Campus Lake and Walden Pond in Baton Rouge as well as marsh ponds in Wax Lake and on Point au Fer Island

Table 4. Distribution of Octospiniferoides chandleri infections in Gambusia affinis among some southern Louisiana aquatic habitats. Incidence is reported as percent. Intensity is the number of worms per host.

Locality	Number Examined	Incidence	Intensity
BATON ROUGE			
Campus Lake	79*	0.0	0.00
Ben Hur Ponds	96	75.0	3.56
Walden Pond	20	0.0	0.00
ATCHAFALAYA BASIN			
Petite Prairie	8	75.0	5.36
Bayou Sorrel	5	0.0	0.00
COASTAL			
Wax Lake	4	0.0	0.00
Marsh Pond[1]	4	0.0	0.00
RIVERS			
Comite River[2]	10	10.0	0.10
Mississippi River[3]	4	0.0	0.00

* An additional 371 G. affinis from Campus Lake used in experimental infections showed no evidence of prior infection.

[1] Point au Fer Island, Atchafalaya Bay

[2] at Greenwell Springs Road

[3] at St. Francisville

were negative. Absence of the infections from these areas is most likely do to absence of suitable ostracod intermediate hosts. O. chandleri, then, is most often found in lentic habitats containing suitable ostracod hosts where the mosquitofish is the most important definitive host.

Interspecific Competition

The mosquitofish in Alligator Bayou were heavily infected with the intestinal trematode Homalometron armatum. The question arose as to whether the presence of this parasite could be responsible for the low numbers of O. chandleri infections. Evidence of competition between these species was sought through analysis of field data and laboratory experiments.

Incidence of H. armatum and O. chandleri calculated from monthly mosquitofish necropsies from Alligator Bayou were used to compute the expected frequencies for mixed infections, single infections for each parasite, and no infections (Hirsch and Gier, 1974). When observed frequencies were compared by X^2 analysis, no significant differences were found ($P < 0.05$). Similarly, when the segregation coefficent reported by Pielou (1969) was calculated using these data, it was found to have a value very close to zero (0.0167). Since a coefficient value of zero indicates no segregation or association, there is no evidence of competition between H. armatum and O. chandleri in presence-absence information from suprapopulation distributions.

In a more sensitive test for associations, the numbers of O. chandleri and H. armatum in concurrent infections were correlated.

The linear correlation coefficient (r) was -0.41 while the log-log correlation coefficient had a value of -0.47. The negative correlation coefficients would indicate avoidance in these two animals but neither correlation was significant ($P < 0.05$).

At the infrapopulation level, there was evidence of competition between H. armatum and O. chandleri. When distributions in the host gut were considered, O. chandleri showed preference for the second quarter of the mosquitofish alimentary tract (gut section 2) in natural concurrent infections (Figure 15). This pattern of distribution was very similar to that exhibited by O. chandleri in single infections (Figure 17). H. armatum, on the other hand, had a bimodal distribution and showed least preference for gut section 2 where O. chandleri were concentrated. Apparently O. chandleri is relatively unaffected by H. armatum presence, whereas H. armatum appears to avoid concentrations of O. chandleri. This avoidance indicates the existence of some form of competition between the two species. Kennedy (1974) reported similar evidence of competition between the acanthocephalan Pomphorhynchus laevis and the caryophyllaeid tapeworm Caryophyllaeus laticeps in bream. In this case, also, the acanthocephalan was least affected by the presence of another parasite. Holmes (1962) found that Moniliformis dubius caused the displacement of the tapeworm, Hymenolepis diminuta, in concurrent infections in rats.

When reciprocal concurrent infections were established experimentally by exposing infection-free mosquitofish to wild infections in cages, the seemingly subtle competition between O. chandleri and H. armatum was shown to reduce both incidence and density of fluke infections (Table 5). Highly significant declines in H. armatum

Figure 15. Distribution of Octospiniferoides chandleri and Homelometron armatum in the alimentary tract of Gambusia affinis during natural concurrent infections in Alligator Bayou.

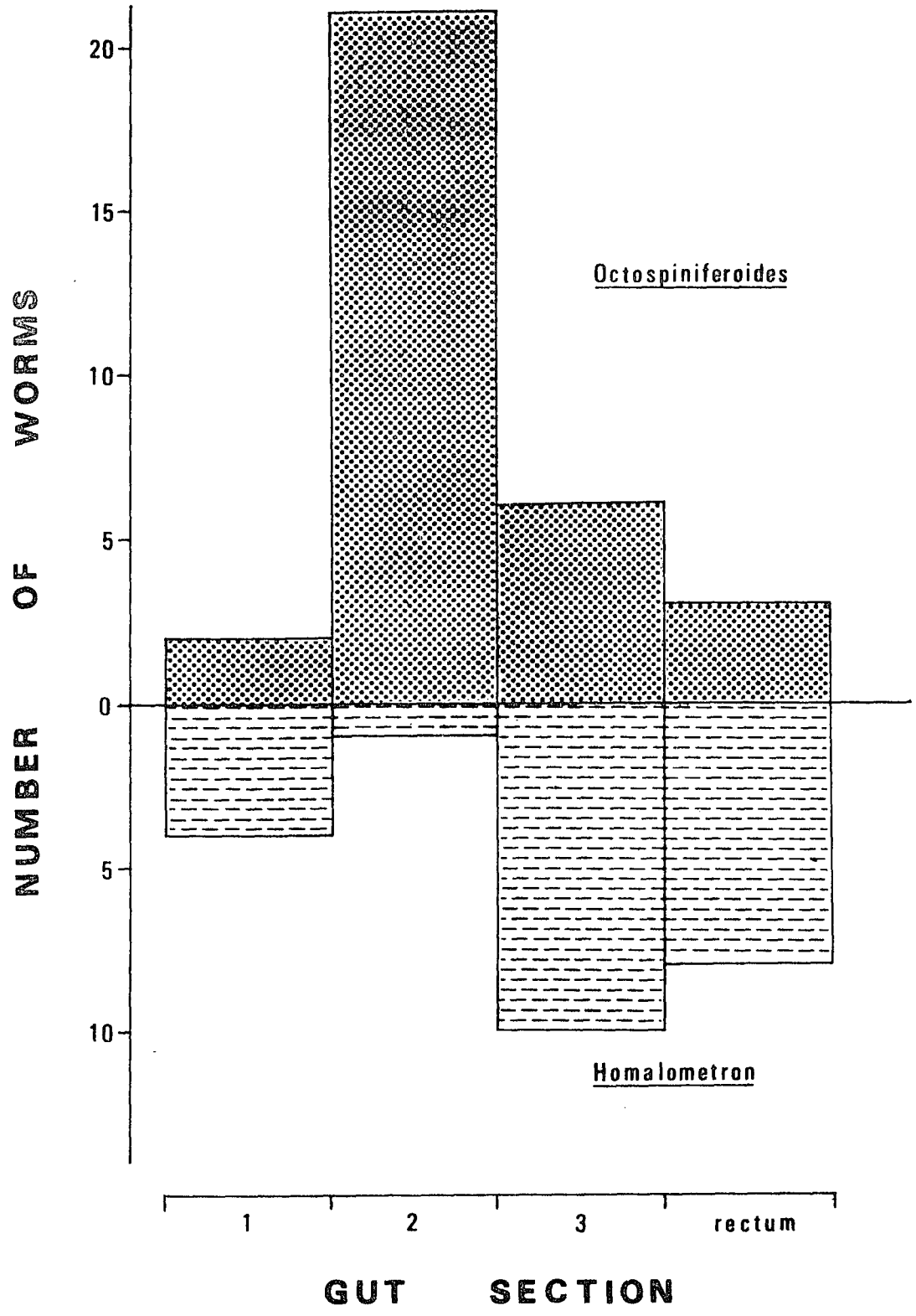

20
15
10
5
0
5
10
NUMBER OF WORMS
Octospiniferoides
Homalometron
1
2
3
rectum
GUT SECTION

Table 5. Incidence and intensity of Homalometron armatum and Octospiniferoides chandleri from experimental concurrent infections in Gambusia affinis. Incidence is reported as percent. Intensity is the number of worms per host. Controls received initial infection only.

Experiment	H. armatum		O. chandleri	
	Control	Treatment	Control	Treatment
I. H. armatum then O. chandleri				
Incidence	73	10**	--	55
Intensity	1.18	0.30*	--	0.70
II. O. chandleri then H. armatum				
Incidence	--	5	30	$25^{N.S.}$
Intensity	--	0.05	1.60	$0.35^{N.S.}$

* significantly different from control at 0.01 level
** significantly different from control at 0.005 level
N.S. not significantly different from control

populations resulted when O. chandleri were superimposed upon them. O. chandleri populations were also reduced by superimposed H. armatum but not significantly ($P < 0.05$). H. armatum had very little success at becoming established when it was the second infection (Experiment II, Table 5). O. chandleri was much more successful as a second infection (Experiment I, Table 5). Evaluation of the significance of second infection success is not possible because the lack of suitable controls precludes statistical analysis.

It seems clear from these observations and experiments that O. chandleri and H. armatum do compete. Competition is probably for space since the different modes of feeding make competition for food unlikely. The evidence assembled here strongly indicates that in concurrent infections O. chandleri has a competitive advantage over H. armatum. Competition, therefore, cannot explain the low infection rates of O. chandleri in habitats which support H. armatum infections. It must be concluded that environmental factors are most important in governing habitat-level spatial distributions of O. chandleri probably through their effects upon intermediate hosts.

Frequency Distributions

The frequency distribution of Octospiniferoides chandleri in the mosquitofish population of Tramline Pond was found to be highly overdispersed indicating aggregation or clumping. When distribution over the entire study was fitted to the negative binomial distribution using the methods of Bliss and Fisher (1953), it was found to best fit the discreet distribution having the parameters, mean (m) = 7.71 and

k = 0.7416. Thus the expected proportion (Px) of the host population harboring x O. chandleri was:

$$P_x = \frac{(K + x - 1)!}{x!(k-1)!} \cdot \frac{R^x}{q^x}$$

where q = 1 + m/k = 11.394 and R = m/(K + m) = 0.9122 (Figure 16). Expected frequencies generated by this expression were tested against observed values using the Komogorov-Smirnov one sample test (Siegel, 1956) and no significant difference was found ($P < 0.05$).

The degree of overdispersion in the O. chandleri distribution is best described by the ratio of its variance to the mean (158.89/7.71 = 20.6). This is a very wide departure from the random Poisson distribution in which the variance is equal to the mean (Fryer, 1966). The log-normal distribution was judged inappropriate for this type of distribution because it does not allow for a zero class. In the study of parasite populations, the zero class (the number or proportion of uninfected hosts) is very important and a diagnostic tool omitting this statistic has minimum value. The logarithmic series distribution recommended for describing parasite data by Williams (1944) also has no provision for including a zero class. Pennycuik (1971b) found that both these distributions fit parasite data from stickleback less well than the negative binomial.

O. chandleri was the most abundant helminth parasite in Tramline Pond and the most over dispersed (Table 6). Other species encountered during the study included two metacercarial trematodes (Posthodiplostomum minimum and Crassiphiala bulboglossa), a larval acanthocephalan (Neoechinorhynchus cylindratus), a larval cestode (Ophiovalipora sp.) and a juvenile nematode (Camallanus oxycephalus).

Figure 16. Frequency distribution of Octospiniferoides chandleri in the Gambusia affinis population of Tramline Pond. Bars represent observed values. Dots represent values predicted by the negative binomial distribution fit to the data by the maximum likelihood method of parameter estimation (Bliss and Fisher, 1953).

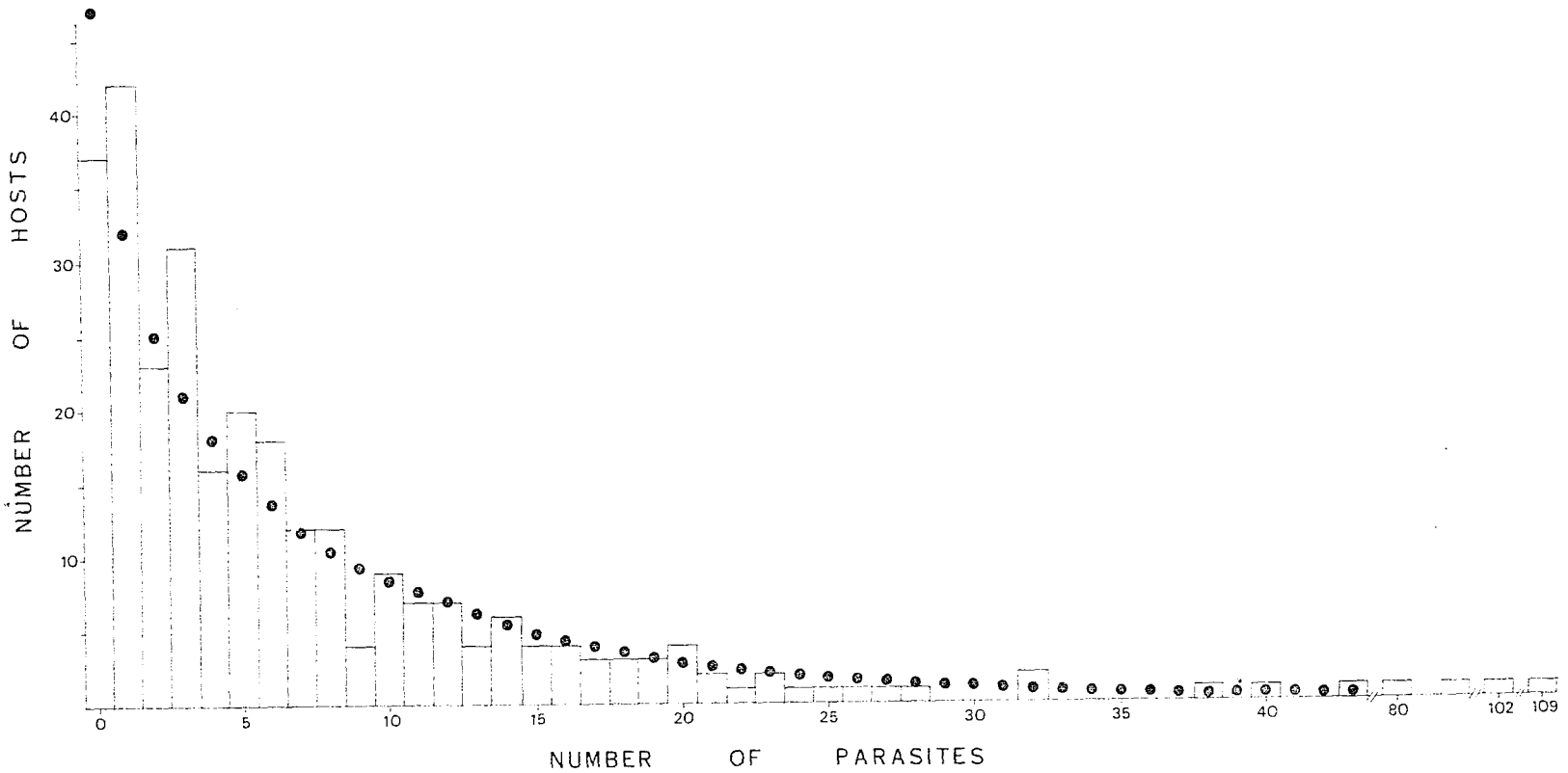

NUMBER OF HOSTS
40
30
20
10
0
5
10
15
20
25
30
35
40
80
102
109
NUMBER OF PARASITES

Table 6. Distribution statistics for the six most abundant helminth endoparasites of Gambusia affinis in Tramline Pond.

Parasite	Number per Host	Percent Infected	Negative Binomial Statistics		
			K	S^2/m	Significance of Fit*
Octospiniferoides chandleri	7.71	87.2	0.742	20.6	0.01
Posthodiplostomum minimum	4.35	72.2	0.771	5.1	0.01
Ophiovalipora sp.	0.34	0.2	0.336	2.0	0.01
Crassiphiala bulboglossa	0.13	0.1	0.093	2.0	0.01
Neoechinorhynchus cylindratus	0.11	0.1	0.755	1.1	0.01
Camallanus oxycephalus	0.09	0.1	0.176	1.8	0.01

* Kolmogorov-Smirnov one-sample test

All of these fit the negative binomial distribution well even though they were not markedly overdispersed. In the N. cylindratus distribution, the mean and variance were approximately equal (S^2/m = 1.1) indicating that the Poisson distribution would be equally appropriate in this case. Obviously, the Poisson and negative binomial distributions converge as the mean and variance approach equality.

Distribution of O. chandleri between individual hosts in Tramline Pond was found to be affected both by host size (age) and host sex. There was a significant correlation between O. chandleri worm burden and G. affinis total length ($P < 0.01$). This kind of observation has been reported repeatedly by many investigators. Pennycuik (1971c) found large stickleback to be more heavily infected than smaller stickleback with N. rulili, Schistocephalus, and Diplostomum. Cloutman (1978) reported a similar relationship for monogentic trematodes on flat bullheads. The three factors that seem to be primarily responsible for this are: 1) accumulation of parasites over a long span of time, 2) greater exposure to parasites due to increased body surface and feeding rates of large fishes, and 3) more physical space to accomodate worms in larger fish.

Effect of Host Size and Sex

Male mosquitofish in Tramline Pond had a mean O. chandleri burden of 2.79 worms over the entire study. The female mosquitofish burden was 9.60 worms per host which was 3.4 times that of males. Not surprisingly, a student's t-test showed the female burden to be significantly larger ($P < 0.0001$).

Male mosquitofish growth virtually halts at sexual maturity (Turner, 1941) while females continue to grow. Thus, the females in any given population are much larger than the males. Since worm burden has been shown to be directly related to host size, it is possible that the difference between host sexes could be due entirely to the disparity in size. Covariance analysis was used to effectively remove the effects of size on worm burden and still female mosquitofish were shown to have a much higher infection intensity than males ($p < 0.0001$).

There remained yet another factor that might account for sex differences in worm burden. While dissecting specimens, it became apparent that much of the body cavity was taken up by large testes and muscular development associated with the gonapodium in maturing males. Also the anus is more anterior in mature males than in females and thus the body cavity in males is proportionally shorter. Alimentary tracts removed from mature males seemed to be shorter and narrower than those from females of comparable length. If this relationship were true, apparent differences in worm burdens might be explainable in terms of differences in the attachment space available to the worms in male and female hosts. This possibility was explored by measuring the excised alimentary tracts of various sized male and female mosquitofish. The measurements were used to calculate the interior surface area of each gut and these were in turn used with fish total length to generate a function relating gut surface area to host total length. The functions for male and female hosts were used to recalculate infection intensities in terms of worms per mm^2 of gut surface area.

Early attempts to work with fresh material provided extremely variable measurements due to the contraction and stretching of gut

tissue. Preserved fishes provided much more consistent measurements which allowed the development of functions with r^2 values of 0.96 and 0.89 for females and males, respectively.

Gut area was found to increase exponentially with total length (L) for both males and females:

$$\text{Females: area} = 0.054\ L^{1.945}$$

$$\text{Males : area} = 0.181\ L^{1.518}$$

These curves diverge at a length of 10 mm and thereafter the rate of increase in males is much less than in females as the exponents in the formulae suggest.

When worm burdens were calculated on a worm/mm^2 of gut surface basis, mean densities were 0.206/mm^2 and 0.101/mm^2 in female and male hosts, respectively. The exercise accounted for some of the differences in female versus male worm burdens and reduced the disparity from a 3.4:1 ratio to a 2.0:1 ratio in favor of females. These parasite densities were still significantly different ($p < 0.0001$).

Male-female differences in worm burden may be a result of differing resistance to infection. More likely it is due to differences in feeding rates between the sexes. Males, preoccupied with courtship most of their lives, eat sparingly on a "maintenance only" diet. Females eat, almost continually. Also, the larger females are better equipped to be cannibalistic and may concentrate O. chandleri in this way. Reduced food intake in males reduces both exposure to O. chandleri infection and ability to maintain a large intestinal fauna.

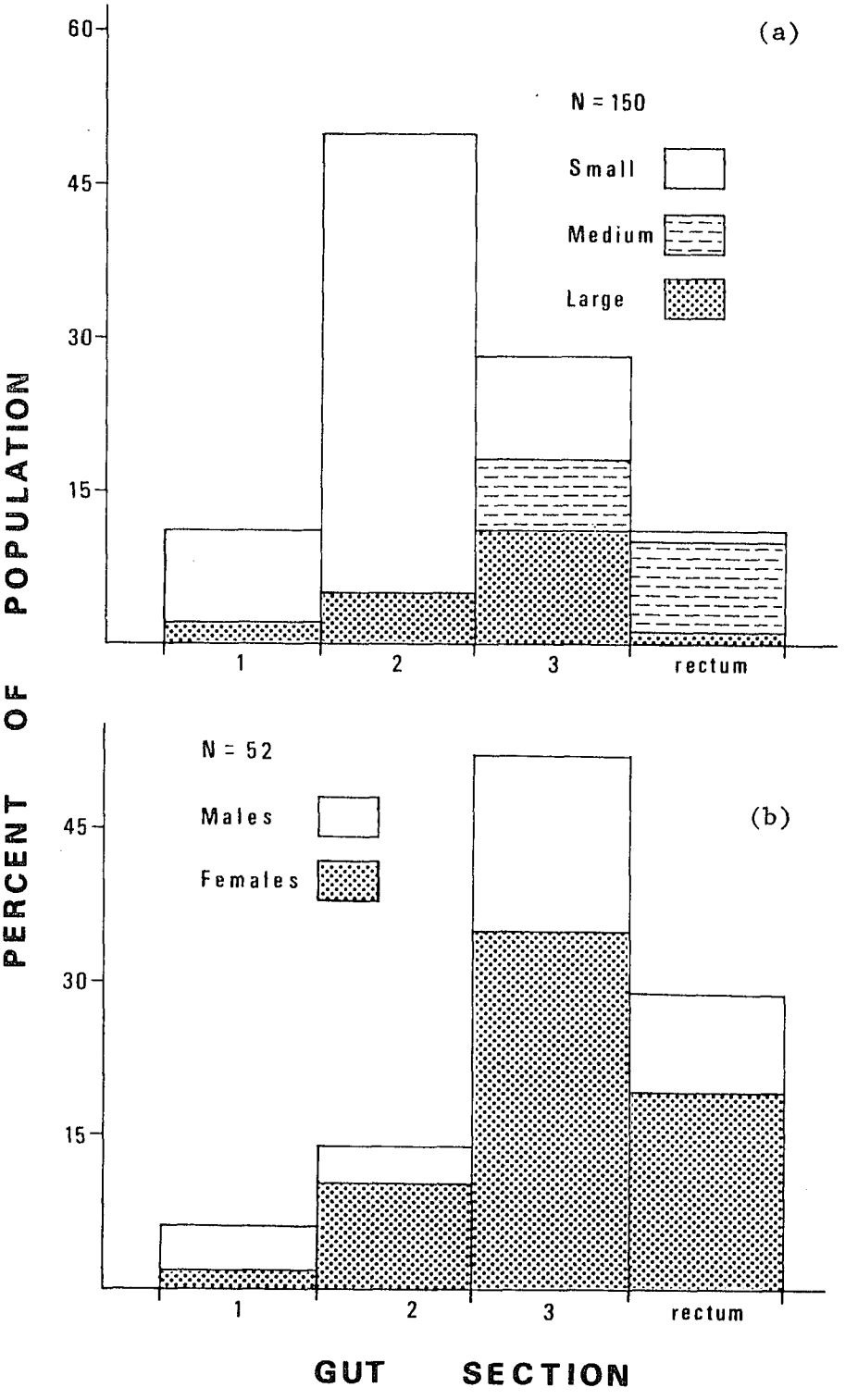
Site Preference

In Tramline Pond, O. chandleri spatial distribution within mosquitofish alimentary tracts was determined by site preference which varied with parasite sex and size.

When several host samples were examined with close attention to the distribution of O. chandleri in four equal-length sections of the alimentary tract, worms were found most frequently in the second section from the interior end. Three hundred and ten worms from five G. affinis collections were distributed as follows: section 1 (anterior) - 9%, section 2 - 76%, section 3 - 12%, and section 4 (rectum) - 2%. Chi-square testing showed that this distribution was significantly different from a theoretical even distribution between sections ($P < 0.001$).

One hundred fifty worms from 35 G. affinis collected in Tramline Pond on March 6, 1976 were sexed and subjectively assigned to small, medium and large size classes as well as recording their position in the host gut. Again, the majority of the worms were found in gut section 2 (Figure 17a). Small worms (1 mm and smaller) constituted the vast majority of O. chandleri in this section. Large worms (2 mm and larger) were most concentrated in section 3 while medium-sized (1 to 2 mm) worms were about equally divided between section 3 and the host rectum. When medium and large male and female worms from the same collection were considered separately, it was obvious that females showed more site preference than males but both were most numerous in section 3 (Figure 17b). The males seemed to occupy sites in the gut generally anterior to females, outnumbering them in section 1 and being outnumbered

Figure 17. Distribution of Octospiniferoides chandleri in the alimentary tracts of Gambusia affinis in Tramline Pond. (a) Distribution by worm size. (b) Distribution by sex of medium and large worms.


(a)
N = 150
Small
Medium
Large
60
45
30
15
1
2
3
rectum
(b)
N = 52
Males
Females
45
30
15
1
2
3
rectum
PERCENT OF POPULATION
GUT SECTION

by them in the rectum. A chi-square test indicated no significant difference between male-female distributions in the host gut ($P < 0.05$).

Clearly, O. chandleri showed site preference that was weakest in young worms of both sexes and strongest in adult females. But the site preference in this worm is believed stronger than the information in Figure 17 indicates. First of all, the 310-worm sample mentioned above contained only 9% and 2% of worms in the extreme anterior section and rectum, respectively. These proportions are much less than the 13% found in each of the extreme regions for the sample chosen for more detailed analysis and figured here. The former proportions are also more in line with my appreciation of O. chandleri distribution from having dissected hundreds of mosquitofish. Secondly, the decision to divide the host gut into four equal sections was made for convenience as the only morphologically distinct section of the alimentary tract was the rectum which happened to be approximately one fourth of the total gut length. This choice may have been unfortunate. Dividing the gut in this fashion puts the first two section boundaries at the first and second flexures in the nearly "S-shaped" gut. The majority of the worms were concentrated very close to this second flexure and placing a boundary in this region artificially partitions a natural mode.

Reduced site preference in young worms has been reported by other investigators. Lewis and Bryant (1976) found that specimens of the nematode, Nematospiroides dubius, were widely scattered as new infections in laboratory mice but became highly aggregated as they matured. Amin and Burrows (1977) found that Echinorhynchus salmonis in several hosts preferred more posterior positions in the gut when

they were mature. Uglem and Beck (1972) described a similar posterior movement related to Neoechinorhynchus cristatus maturation. He found the position in the gut to be related to the host secretion of aminopeptidases. Decrease in aminopeptidase activity with age was accompanied by an increase in both host and site specificity. Mature worms prefered sites with host aminopeptidase activity.

Summary of Spatial Distributions

Octospiniferoides chandleri is found most frequently in lentic habitats where the major definitive host is the mosquitofish, Gambusia affinis. Fundulus olivaceous and Fundulus chrysotus are also suitable definitive hosts and constitute new host records. The trematode, Homalometron armatum, does not compete successfully with O. chandleri and is not an important factor limiting O. chandleri populations in streams. Low population levels of the acanthocephalan in streams is most likely due to environmental factors which limit ostracod host populations.

In Tramline Pond, O. chandleri has an overdispersed or contagious distribution among mosquitofish hosts which is well described by the negative binomial distribution. Among individual hosts, O. chandleri infections increase with host size and female mosquitofish are more heavily infected than males. Within individual mosquitofish, the acanthocephalan is most abundant in the second quarter of the gut. Females and older worms show more pronounced site preference and tend to be distributed closer to the anus than males and younger worms.

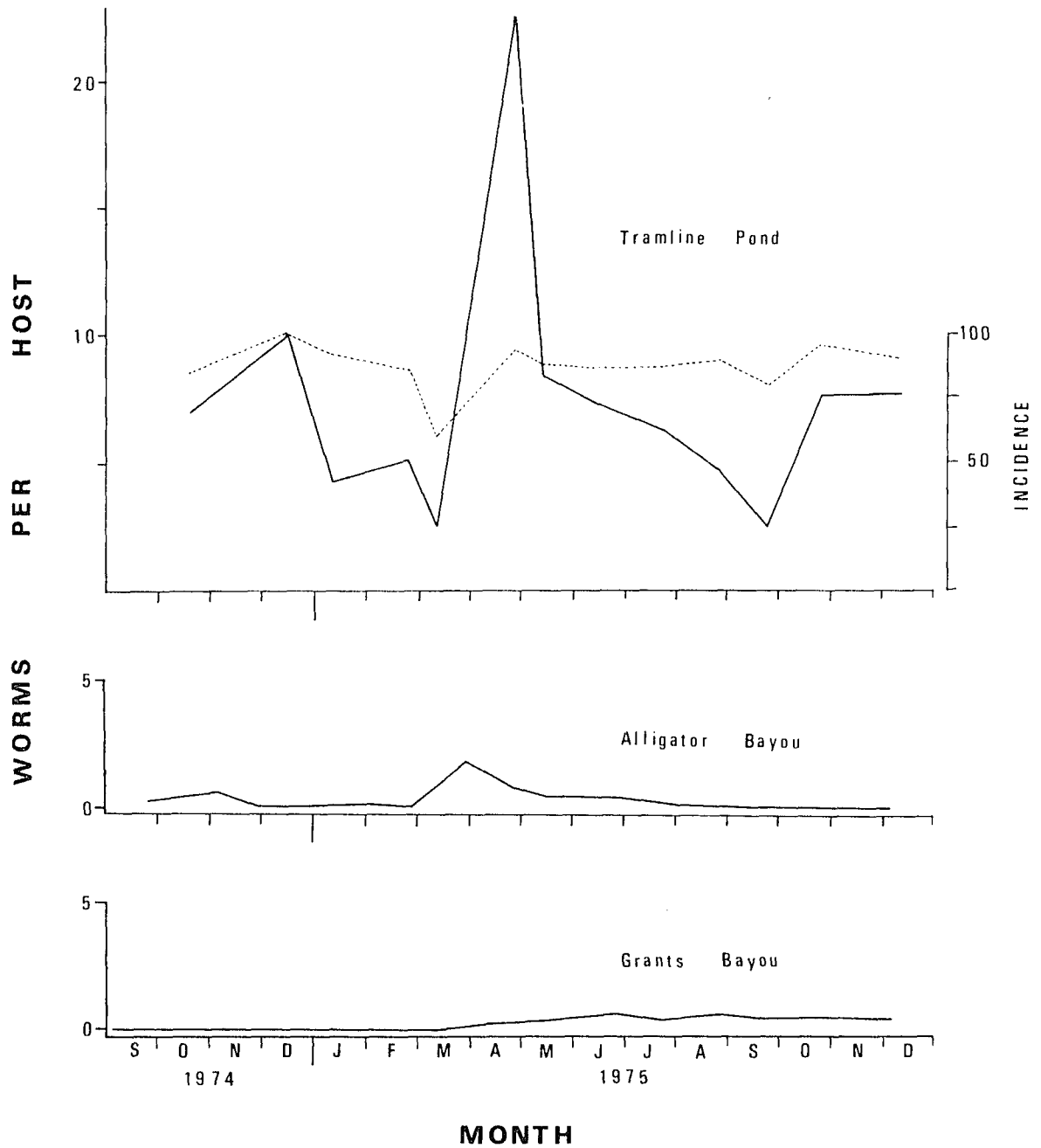
Temporal Distributions

Seasonal Changes in Abundance and Maturation

Temporal changes in Octospiniferoides chandleri infections in mosquitofish from Tramline Pond, Alligator Bayou and Grants Bayou are shown in Figure 18. Incidence of O. chandleri in Tramline Pond varied little over the study period. A slight decline in the percent of hosts infected during the winter months was followed by a sharp rise in the spring. But since the incidence deviated little from 90% over the year period, it provided little evidence of seasonality. On the other hand, intensity of infections did appear to have a definite seasonal pattern. Intensity seems to mirror the slight changes in incidence, falling off during the winter and rising steeply in the spring. Infection intensities slowly declined during the summer and rose slightly in the fall.

Infection intensities in Alligator and Grants Bayou were extremely low over the study period and showed few fluctuations. In Alligator Bayou, infection intensities were lower in the winter of 1974-75 than in the fall and a spring peak was nearly coincident with the large spring increase in Tramline Pond. Grants Bayou had no O. chandleri infections during the first seven months of the study and then infection intensities rose to a rather steady value of 0.5 to 0.8 worms per host for the remainder of the study period. The appearance of the infection in Grants Bayou in the second year of the study was probably due to the fact that 1975 was a dry year. During much of the time there was no flow in the bayou and the fauna of the stream

Figure 18. Seasonal changes in mean intensity of *Octospiniferoides chandleri* infections in *Gambusia affinis* from Tramline Pond, Alligator Bayou, and Grants Bayou, September, 1974 - December, 1975. The dashed line in the Tramline Pond graph represents the incidence or the percent of hosts infected.


WORMS PER HOST
20
10
Tramline Pond
100
50
INCIDENCE
5
0
Alligator Bayou
5
0
Grants Bayou
S O N D J F M A M J J A S O N D
1974
1975
MONTH

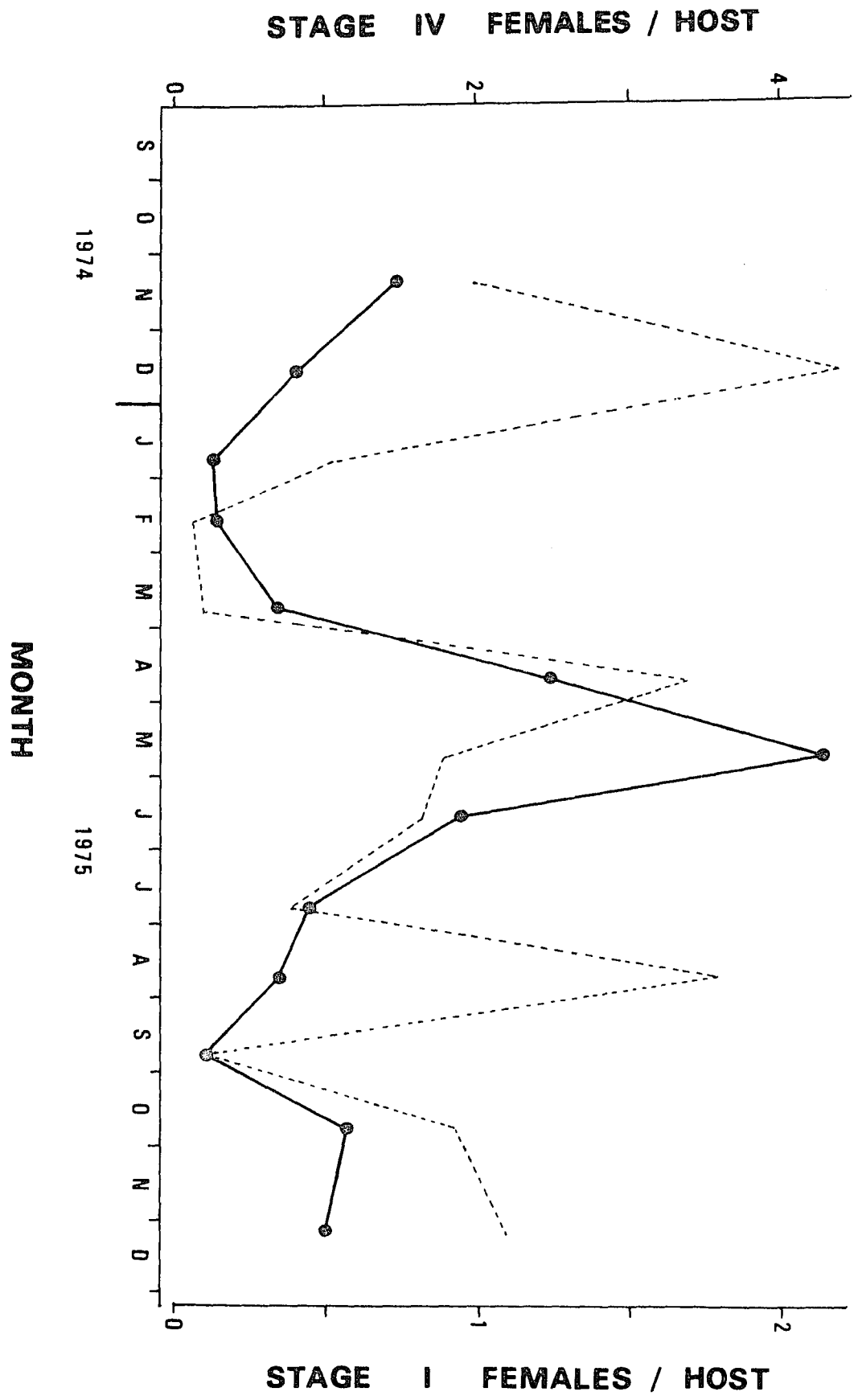
was confined to a series of small pools. These lentic habitats probably allowed the development of potential intermediate host (ostracod) populations. The infection could then have spread from base level portions of the stream by mosquitofish migration during infrequent spates.

The O. chandleri data collected from Tramline Pond mosquitofish were analysed to provide information on temporal changes in worm size, sex ratios, and in densities of Stages I and IV female worms. All of these have become established methods of examining parasite data for evidence of seasonality.

When the reproductive status of Tramline Pond O. chandleri was investigated by plotting the density of Stage IV females over time, a very well defined peak appeared in April and May of 1975 (Figure 19). Stage IV female density declined through the summer to a low in September. The density of Stage I females showed three peaks in December, 1974, April, 1975 and August, 1975. These data seem to indicate three periods of recruitment during the year.

Mean sizes of male and female worms changed little over the study period and both sexes remained below their respective midranges of 2.18 mm for females and 1.11 mm for males throughout most of the study indicating the continual presence of a young population (Figure 20a). Mean male sizes were always smaller than those for females and generally followed changes in female mean size. Although there were no dramatic changes, notable features of the size plots included a sharp rise in the early spring followed by a decrease which corresponded to the spring increase in density (Figure 18). This suggests that an influx of young worms into the population occurred at that

Figure 19. Seasonal changes in mean intensity of Stage I (dashed line) and Stage IV (solid line) female *Octospiniferoides chandleri* in *Gambusia affinis* from Tramline Pond, November 1974 - December 1975.


STAGE IV FEMALES / HOST
0
2
4
S O N D J F M A M J J A S O N D
1974
1975
MONTH
0
1
2
STAGE I FEMALES / HOST

time. Worms of both sexes were generally larger in the early summer months and smaller in the late summer and fall.

Monthly estimates of sex ratio in the O. chandleri population fluctuated tremendously over the study period and rose above one only in January and July of 1975 (Figure 20b). Since most female acanthocephalans live longer than males, male/female ratios are generally less than one and peaks in the sex ratio indicate the presence of young populations. These identify prime times of recruitment. Pennycuik (1971a) used this method with some success to examine seasonal phenomena in Echinorhynchus clavula infections in stickleback. The O. chandleri sex ratio data seem to have no interpretable patterns.

The information available on the seasonality of acanthocephalan parasites of fishes is summarized in Table 7. Acanthocephalan seasonality seems to be absent or inconspicuous in homoiothermal vertebrates (Nickol, 1966; Karl, 1967), although Denny (1968) found that populations of Polymorphus marilus in the lesser scaup increased through the summer and declined in the fall.

Acanthocephalan seasonality in fishes is composed of two principal components; a seasonal maturation cycle and seasonal changes in density. The acanthocephalan cycle usually includes fall infections, growth and maturation in winter and spring, and egg production and death in summer months. This simple scheme is complicated by the fact that some representatives of all stages of development are usually present in every month of the year (Awachie, 1965). Seasonal changes in acanthocephalan population density may be pronounced or undetectable. Modern quantitative studies usually report seasonal variations in infection intensities. Earlier studies tend to be

Figure 20. Seasonal changes in some characteristics of the *Octospiniferoides chandleri* population in *Gambusia affinis* from Tramline Pond, October 1974 - December 1975. (a) Changes in mean length of male (dashed line) and female (solid line) worms. (b) Changes in the male/female ratio. The dashed line represents the 1:1 ratio, while the light dotted line represents the mean sex ratio for all worms collected.

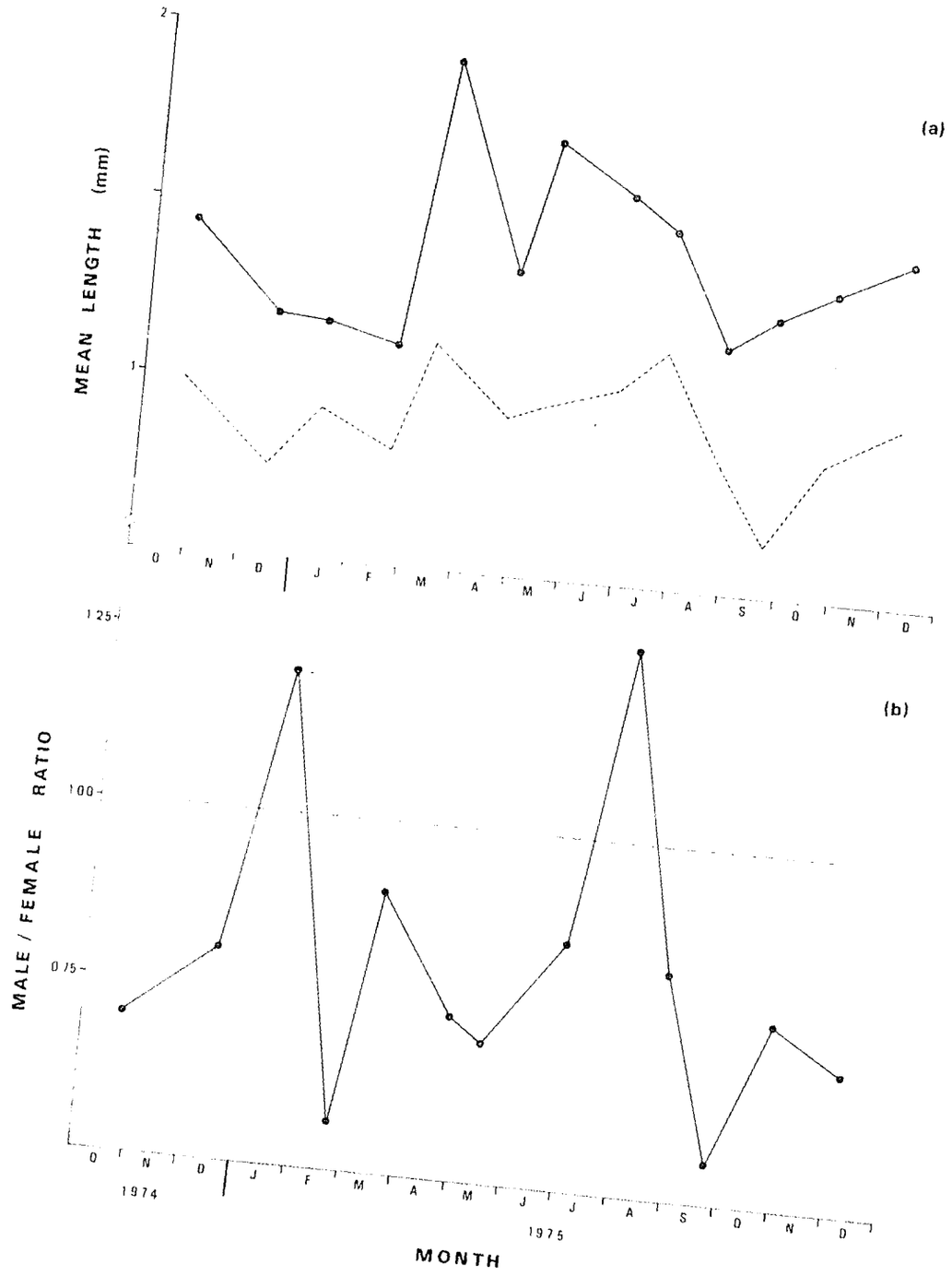

(a)
MEAN LENGTH (mm)
2
1
125
O N D J F M A M J J A S O N D
(b)
MALE / FEMALE RATIO
100
075
O N D J F M A M J J A S O N D
1974
1975
MONTH

Table 7. Seasonal changes in population parameters and maturation in acanthocephalan parasites of fishes.

Acanthocephalan	Peak Incidence	Peak Intensity	Peak Maturation	Peak Recruitment	Authority
PALAEACANTHOCEPHALA					
Echinorhynchus salmonis	spring	winter	summer	fall	Tedla & Fernando, 1969, 1970
" "	winter	winter	spring	winter	Amin & Burrows, 1977
" "	none	none	spring	summer	Amin & Burrows, 1977
" "	none	summer	summer	--	Bauer & Nikolskaya, 1957
Echinorhynchus gadi	spring	spring	--	--	James & Srivastava, 1967
" "	winter	--	summer	fall	Shulman & Shulman-Albova, 1953
" "	none	none	--	--	Polyanski, 1955
Echinorhynchus truttae	winter	summer	spring	summer	Awachie, 1965
Acanthocephalus clavula[1]	winter	winter	winter	fall	Pennycuik, 1971a

Table 7. Continued.

Acanthocephalan	Peak Incidence	Peak Intensity	Peak Maturation	Peak Recruitment	Authority
Acanthocephalus clavula	spring	spring	spring	--	Andrews & Rojanapaibul, 1976
" "	none	none	summer	none	Chubb, 1964
Acanthocephalus parksidei	--	--	spring	fall	Amin, 1977
" "	spring	spring	--	--	Amin, 1975
Acanthocephalus lucii	spring	spring	summer	fall	Komarova, 1950
Acanthocephalus jacksoni	--	spring	spring	fall	Muzzal & Rabalais, 1975
Leptorhynchoides thecatus	--	summer	--	--	DeGiusti, 1949
" "	spring	--	--	--	Cannon, 1973
Pomphorhynchus laevis	spring	spring	--	--	Hine & Kennedy, 1974
EOACANTHOCEPHALA					
Neoechinorhynchus rutili	--	fall	--	--	Merritt & Pratt, 1964
" "	none	none	spring	winter	Walkey, 1967

Table 7. Continued.

Acanthocephalan	Peak Incidence	Peak Intensity	Peak Maturation	Peak Recruitment	Authority
Neoechinorhynchus rutili	fall	fall	spring	fall	Steinstrasser, 1936
" "	winter	none	--	summer	Chappell, 1969
Neoechinorhynchus cylindratus	none	--	summer	fall	Eure, 1974
Neoechinorhynchus spp.[2]	--	winter	--	fall	Bourque, 1974
Gracilisentis gracilisentis[3]	fall	fall	winter	fall	VanCleave, 1916
Tanaorhamphus longirostris	winter	winter	--	summer	VanCleave, 1916
Paulisentis fractus	--	--	summer	fall	Cable & Dill, 1967

[1] reported as *Echinorhynchus clavula* (see Grabda-Kazubska & Chubb, 1968)

[2] a complex of four species dominated by *N. pseudemydis*

[3] reported as *Neoechinorhynchus gracilisentis* (see Petrochenko, 1956)

[4] reported as *Neoechinorhynchus longirostris* (see Petrochenko, 1956)

nonquantitative and seasonality is discussed in terms of incidence cycles. Seasonal changes in incidence are usually minimal except in areas of harsh winters (Chubb, 1964).

The O. chandleri population in Tramline Pond mosquitofish seems to meet the expectations generated by the studies outlined in Table 7. Infection incidence is constant as expected in a warm climate, but changes in worm density do show a rather well-defined seasonal pattern (Figure 18). The most conspicuous and best documented feature of O. chandleri seasonality is the pulse of recruitment that took place in spring, 1975. The occurrence of this recruitment is supported by a marked increase in population density in April (Figure 18), a simultaneous decrease in mean worm size (Figure 20a), and a peak in the density of Stage I females (Figure 19). December and August recruitment, which seem to be indicated by peaks in Stage I female density (Figure 19), are poorly supported by concomitant information even though recruitment during these periods is reported by many authors (Table 7).

Recruitment and Mortality Rates

Failure of the patterns in Figures 19 and 20 to match up in some logical way makes this traditional interpretation of acanthocephalan recruitment suspect and indicates that a more sophisticated analysis is necessary to elucidate seasonal dynamics. The first step in refining the investigation of recruitment rates required defining the infective stage well and narrowing it to a very early portion of the acanthocephalan life cycle. This was done in the life cycle

section by defining the four stages of female development. The Stage I female was designated the infective stage and assumed to represent one-half of the new recruits (assuming a 1:1 sex ratio). The second step involved the determination of temperature effects upon the duration of the Stage I condition since the development rates are affected by temperature and changes in the duration of the Stage I condition would affect the validity of recruitment estimates.

The accumulation rate of Stage I females was calculated by dividing the number collected each month by the duration (days) expected at the temperature for the time of collection (Figure 2). Assuming a 1:1 sex ratio, this rate (multiplied by two to account for males) produced an estimate of the recruitment rate for the period just prior to the time of collection.

Changes in density (ΔD) were calculated by subtracting each monthly estimate of density (mean infection intensity) from the value of the previous month. This ΔD was divided by the number of days between sampling dates to provide the mean daily rate of change over the interim period. Since this method assumes linearity, this mean rate of change is most representative of the midpoint between sample dates and is plotted in this way.

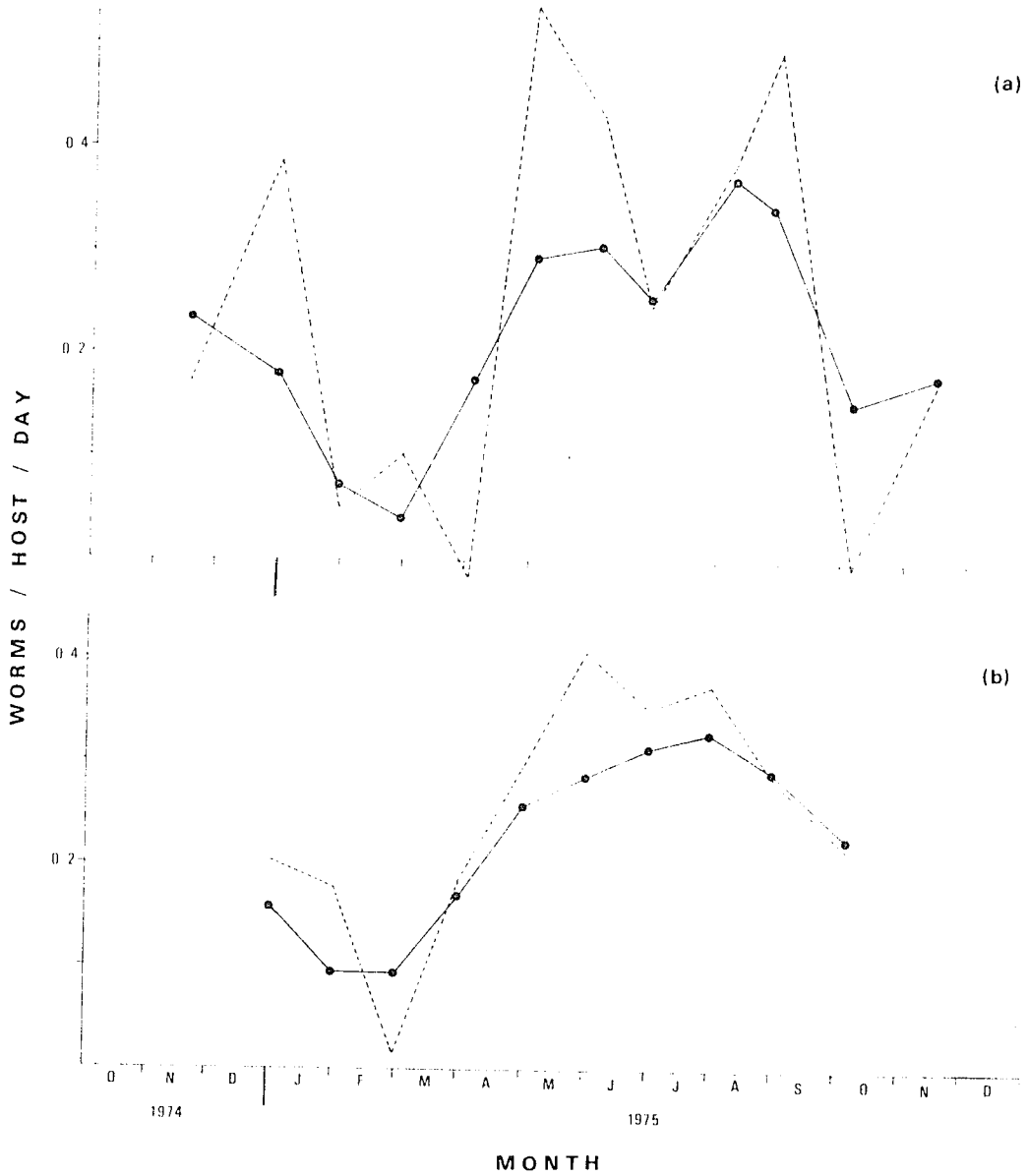
Since no immigration or emigration is possible in the closed system of Tramline Pond, the rate of change of density is due solely to the balance of recruitment and mortality rates. Therefore, mortality can be calculated by merely subtracting rate of change of density from recruitment rate. But since the recruitment rate estimates best represent the period just prior to the second sample in each pair of observations and estimates of rate of change of density best represent

a point in time midway between samples, these two factors must be brought into coincidence by taking the mean of adjacent recruitment estimates to use in the calculation or mortality.

Recruitment and mortality rates calculated from Tramline Pond O. chandleri data are shown in Figure 21. Recruitment rate has some positive value over the entire year (Figure 21a). This is consistent with the observation that Stage I females were present in collections in every month of the year (Figure 19). Beyond this single point, the calculated recruitment rates in Figure 21a show a very different pattern of recruitment changes throughout the year than that suggested by Figure 19. The long duration of Stage I females during the cold winter months eliminates the winter peak in recruitment by accounting for the density of young worms during that period. Similarly, the short duration of Stage I during summer accounts for low density in midsummer and considerably elevates estimates of recruitment during this period. This pattern of lowest recruitment during the late winter and rather continuous high recruitment in the warm months corresponds well to fluctuations of the parental population as indicated by the density of Stage IV females in Figure 19. With larval development time in the ostracod host as short as 20 days (probably less at ambient summer temperatures), we might expect quite a bit of coincidence in the adult and juvenile cycles.

Calculated mortality rates for O. chandleri are quite variable (Figure 21a). This is expected since the errors in estimation of density and recruitment are additive and all fluctuations tend to accumulate in the calculated mortality term. In the early spring and fall, negative values of mortality are generated when recruitment rate

Figure 21. Seasonal changes in recruitment (solid lines) and mortality rates (dashed lines) of Octospiniferoides chandleri calculated from temperature-adjusted acquisition rates of Stage I females and monthly estimates of density (intensity). (a) The curves as calculated. (b) The curves after smoothing by the ratio-to-moving-average method (Alder and Roessler, 1968).


(a)
(b)
0 4
0 2
WORMS / HOST / DAY
O N D J F M A M J J A S O N D
1974
1975
MONTH

estimates do not fully account for the rates of increase of density. In general, though, the pattern of mortality rates seems to follow that of recruitment rates. This was especially evident when the curves in Figure 21a were smoothed using the ratio-to-moving-average method (Alder and Roessler, 1967) (Figure 21b). Mortality rates were lowest in the early spring when the population in Tramline Pond reached its highest density (Figure 18) and was generally higher than recruitment during summer when the population was declining. Both the recruitment and mortality rates explain the observed changes in density over a year but the general pattern they suggest is a sharp departure from that indicated by more conventional interpretations of the data which do not measure or consider the effects of temperature upon development rates.

Since mortality rates were higher during summer and since Kennedy (1972) has shown high temperature to have an adverse effect upon the establishment of acanthocephalans, an attempt was made to relate mortality rate to temperature with regression analysis. The resulting weak positive correlation was not significant ($r^2 = 0.15$, $P < 0.05$). The relationship between mortality rates and water temperature was further investigated by dividing the monthly estimates of mortality rates into two groups based upon their mean monthly water temperatures. The mean mortality rates between the two groups were tested using an independent t-test. Cold months ($\leq$17 C) had a mean mortality rate of 0.163 worms per host per day, while the warm months (>17 C) had a significantly higher mean mortality rate of 0.395 worms per host per day ($P < 0.05$). Mortality rates, then, were significantly higher during the warmer months, but the amount of noise in the data precluded

determining a quantitative relationship between water temperature and mortality rate.

The highest mortality occurred in April coincident with the highest density of O. chandleri observed during the study. This seems to suggest density-dependent mortality caused by intraspecific competition among new recruits and between new recruits and established worms. This kind of mortality has been demonstrated for many helminths.

Agreement of Parasite and Host Seasonal Patterns

The recruitment rate pattern makes sense in terms of parasite strategy when events in the seasonal patterns of the definitive host are considered. Reproductive activity in the Tramline Pond mosquitofish population began in March of 1975 and continued into October (Table 8). The percent of females in the population that contained either developing yellow ova or embryos was highest in the spring and tapered off through the summer and into the fall. Brood sizes also decreased through the reproductive season (Table 8). Mean brood size dropped dramatically when the first young-of-the-year females entered the adult population. The reproductive patterns were similar for mosquitofish in other parts of the Alligator Bayou drainage but they were less well-defined because several different mosquitofish populations were involved (Table 9).

Young-of-the-year mosquitofish first appeared in samples in April of 1975 (Figure 22). At that time, the population was comprised almost entirely of adult males and females. By May, the first wave of young fish had grown considerably and were merging with the smallest

Table 8. Reproductive states of female Gambusia affinis larger than 26 mm (total length) in Tramline Pond, October, 1974 - December, 1975. Females were considered to be reproductively active if either developing yellow ova or embryos were present but only those containing embryos were included in the calculation of mean mother size.

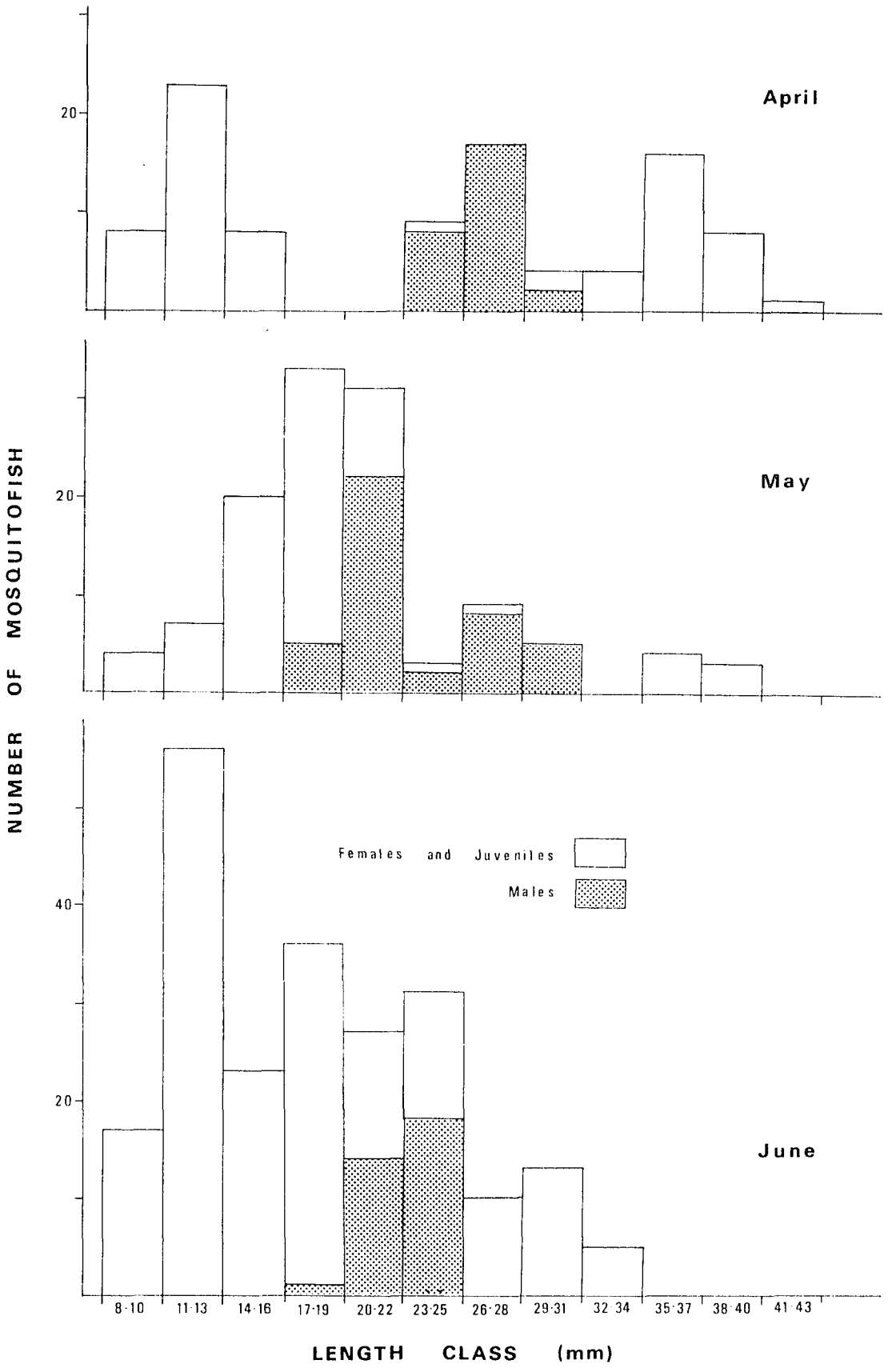
Month	Number Examined	Percent Active	Mean Brood Size	Mean Mother Size
October	12	0.0	--	--
December	6	0.0	--	--
January	6	0.0	--	--
February	8	0.0	--	--
March	6	50.0	21.7	35.7
April	22	100.0	20.4	36.2
May	7	100.0	23.0	37.8
June	22	91.0	9.5	30.3
July	9	77.8	8.4	33.6
August	7	71.4	5.4	30.6
September	11	27.3	9.3	34.3
October	22	4.5	5.0	41.0
December	25	0.0	--	--

Table 9. Reproductive states of female Gambusia affinis larger than 26 mm (total length) in Alligator Bayou and Grants Bayou, September, 1974 - December, 1975. Females were considered to be reproductively active if either developing yellow ova or embryos were present.

Month	Number Examined	Percent Active	Mean Brood Size
September	13	7.7	12.0
October	19	0.0	--
December	19	0.0	--
January	29	13.8*	--
February	20	0.0	--
March	15	46.7	44.3
April	15	93.3	28.3
May	14	92.9	35.1
June	16	75.0	41.2
July	15	100.0	29.3
August	17	76.5	20.6
September	14	64.3	35.3
October	17	5.9	8.0
December	15	0.0	--

* Four of 11 females collected in the Grassy Lake section of Alligator Bayou contained 12-16 developing yellow ova.

Figure 22. Spring changes in size distribution of *Gambusia affinis* in Tramline Pond.


April
May
June
20
20
40
20
Females and Juveniles
Males
NUMBER OF MOSQUITOFISH
8-10
11-13
14-16
17-19
20-22
23-25
26-28
29-31
32-34
35-37
38-40
41-43
LENGTH CLASS (mm)

members of the overwintering population. The largest overwintering mosquitofish were beginning to disappear and by June no female over 34 mm TL was found in a rather large sample. A second wave of mosquitofish recruits were entering the population by June.

The above patterns show clearly that the majority of reproduction in the mosquitofish population takes place in the spring and that by late spring, young-of-the-year fish almost replace the overwintering population in the pond. Since nearly all of the overwintering population and most of the young-of-the-year fish born early in the spring can be expected to die during the summer (Krumholz, 1948), the perpetuation of the O. chandleri population is assured when the offspring of the worms in the overwintering mosquitofish can infect the earliest young-of-the-year fish in the spring. This new generation of O. chandleri matures and reproduces as its host does during summer and guarantees that there will be a source of infection for those mosquitofish born late in the summer and destined to become the next overwintering population.

Effect of Host Feeding Behavior

Since O. chandleri infections are acquired through the food web, the food habits of the Tramline Pond mosquitofish population were investigated (Table 10). The most common item of food, found in 119 of the 187 fish which contained food, was unidentifiable detrital material. Microcrustaceans, especially cladocerans, however, were most often recorded as contributing the greatest volume to the gut contents. Terrestrial and aquatic insects, because of their large size,

Table 10. Frequency of food items in the alimentary tracts of Gambusia affinis from Tramline Pond, October, 1974 - December, 1975. One hundred of 287 fish examined contained no food.

Food Item	Frequency	
	Number	Percent
Detritus	119	63.6
Algae	57	30.5
Cladocera	46	24.6
Ostracoda	34	18.2
Bryozoa (floatoblasts)	22	11.8
Insecta (terrestrial)	21	11.2
Protozoa	19	10.2
Insecta (aquatic	18	9.6
Rotifera	10	5.3
Copepoda	5	2.7
Collembola	5	2.7
Scum	3	0.2
Hydracarina	3	0.2
Arachnida	2	0.1
Vascular plant material	2	0.1
Others (Gastropoda, Oligochaeta, fish and fish scales)	3	0.2

were probably the second most important food items in terms of volume. Barnickol (1941) and Rice (1942) both found microcrustaceans and insects to be the dominant food items in the diet of mosquitofish in Reelfoot Lake. In Tramline Pond mosquitofish, bryozoan floatoblasts were frequently the predominant food item in the late summer and fall collections.

Ostracods were the fourth most frequently encountered food in mosquitofish from Tramline Pond and were rarely the predominant item in any single fish. Ostracods were more frequent in the diet of Tramline Pond mosquitofish in the spring months than during the summer and fall (Table 11). This, of course, is the time of year in which recruitment rates initially increased (Figure 21). Walkey (1967) found that stickleback fed most heavily upon ostracods in the summer and fall coincident with the acquisition of new infections of Neoechinorhychus rutili. He concluded that this was not as important as temperature in determining the annual cycle in the worm. In the case of O. chandleri, host feeding behavior probably has little effect upon seasonality. Ostracods seem to reproduce rapidly in the spring, both in the laboratory and in the field. These new additions to the ostracod population would be expected to dilute O. chandleri infections and offset the effect of increased mosquitofish predation upon the acquisition of new parasites.

Demography

Development of the age-size regression for known age male and female O. chandleri (Figure 13) allowed assigning ages to worms

Table 11. Seasonal changes in Gambusia affinis ostracod predation in Tramline Pond, October, 1974 - December, 1975.

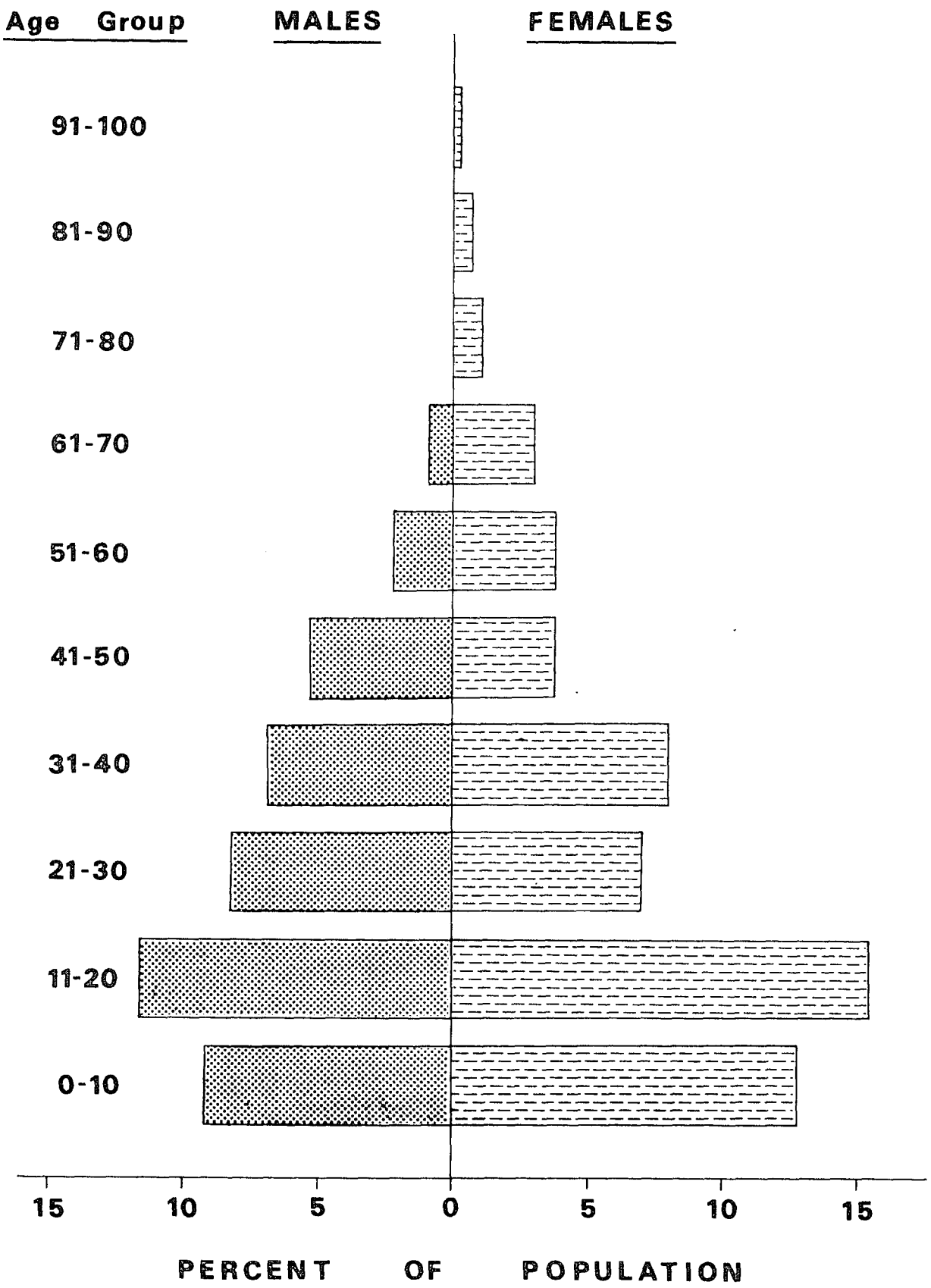
Season	Number Examined	Guts Containing Ostracods	
		Number	Percent
Spring (Mar, Apr, May)	75	18	24.0
Summer (Jun, Jul, Aug)	75	4	5.3
Fall (Sep, Oct, Nov)	73	3	4.1
Winter (Dec, Jan, Feb)	64	8	12.5

collected from Tramline Pond during the study. Arraying the frequency of males and females in 10-day age groups produced a broad-based pyramid indicative of a young population. It also showed clearly that female worms live much longer than males (Figure 23). Some females had estimated ages of nearly 100 days while no male over 70 days old was found. Similar differences in the longevity of male and female acanthocephalans have been reported for Moniliformis dubius in rats (Burlingame and Chandler, 1941) and Octospinifer macilentis in suckers (Harms, 1965). Many other authorities have also expressed belief that female acanthocephalans live longer than males (Amin, 1977; Nickol and Heard, 1973; Pennycuik, 1971d; Steinstrasser, 1936).

The 0-10 day age class was expected to be larger than the others. Its relatively small size could result either from a more rapid growth to the next class than the linear model predicts or early mortality causing many new recruits to be missed in sampling. Rapid growth during this period seems unlikely. Although obscured in Figure 13 by several superimposed sets of data, new experimental infections characteristically had a one- to three-day lag period before growth began. Thus, linear expectation of size during this period would tend to overestimate rather than underestimate growth rate. Early mortality therefore is the best explanation of this distribution.

Females were more abundant among the youngest and oldest worms. This is easily explained for the older worms by the increased longevity of females. The differences in small size classes were not large and may have been artificial. There is no evidence to suggest that development in the ostracod host favors one sex over another and most authors report 1:1 sex ratios in larval acanthocephalans (Crompton,

Figure 23. Age distribution by sex for 990 Octospiniferoides chandleri collected from Gambusia affinis in Tramline Pond October, 1974 - December, 1975. Ages in days were estimated from age-size regressions (Figure 13).


Age Group
MALES
FEMALES
91-100
81-90
71-80
61-70
51-60
41-50
31-40
21-30
11-20
0-10
15
10
5
0
5
10
15
PERCENT OF POPULATION

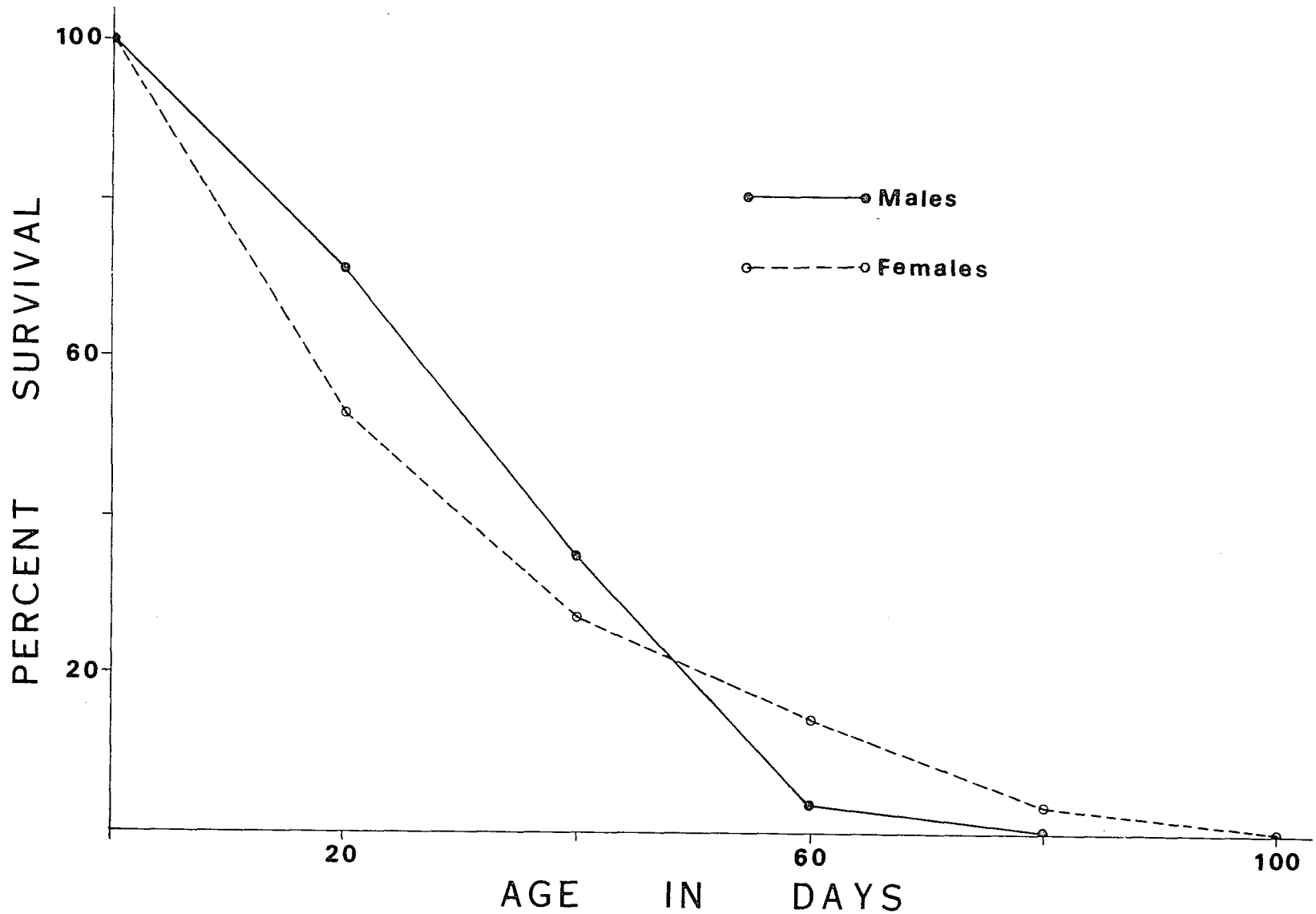
1970). Kennedy (1972) found that males of Pomphorhynchus laevis were less successful at becoming established in the gut of goldfish females. This may also be true for O. chandleri. The sharp decline in females at the third age group is difficult to explain. This occurred at a time when female worms were undergoing rapid ovarian ball proliferation and some were copulating. These activities may have caused some additional mortality.

Mortality rate changes with age were best visualized when adjacent age groups were combined and a survivorship curve constructed (Figure 24). It can be seen that males have a rather constant mortality throughout their life while females have a higher initial mortality rate which quickly declines to less than the value for males. Females of Pomphorhynchus laevis also have higher initial mortality than males (Kennedy, 1972).

Summary of Temporal Distributions

On the basis of traditional analysis of such information as seasonal changes in incidence, density, population reproductive state, mean worm size, and sex ratio, O. chandleri seems to have a seasonal pattern very much like those previously reported for other acanthocephalans. But a slightly different and more realistic pattern is produced when the data are adjusted to account for the effect of temperature upon the duration of early parasite stages. After the proper adjustments, it is clear that the majority of reproductive activity takes place in spring and summer. Peaks and nadirs of mortality correspond with those of recruitment. This pattern coincides well with

Figure 24. Survivorship curves for Octospiniferoides chandleri males and females based on age distribution in Figure 23.


100
60
20
PERCENT SURVIVAL
Males
Females
20
60
100
AGE IN DAYS

the seasonality of the mosquitofish host. Control of the seasonal pattern is probably due to the direct or indirect effect of temperature upon the worm with changes in host feeding behavior playing a minor role.

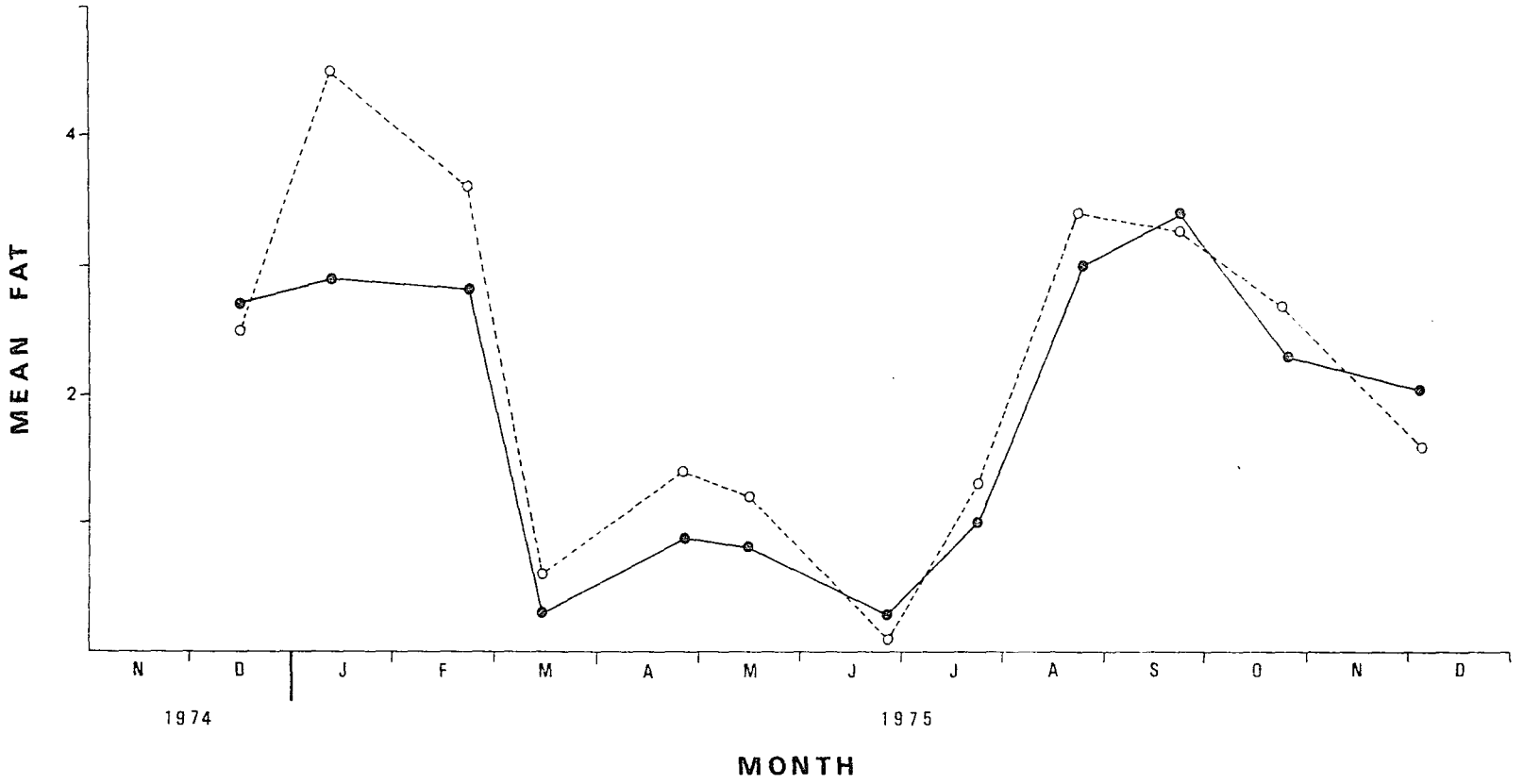
Effects upon the Host

I found no evidence of pathology or debilitation during host necropsies that could be related to O. chandleri infections. Bullock (1967), in his histological examination of the alimentary tracts of mosquitofish infected with O. chandleri, found no pathology except for minor tissue damage at the point of entry of proboscis hooks. Hooks never penetrated beyond the epithelium and there was no evidence of host reaction. In the absence of any evidence of pathology, I attempted to discover the more subtle effects of O. chandleri on the host. I reasoned that any effect on the general well-being of the host might be reflected in fat storage or fecundity.

Effect upon Fat Storage

The extent of the mesenteric fat deposition in each fish examined was evaluated subjectively and assigned a number value from zero (no fat) to 10 (maximum fat). The fat index values thus obtained varied widely within collections but their mean values produced well-defined patterns (Figure 25). Fat accumulation was highest in the winter months, especially in females, and low in summer. It dropped precipitously at the onset of the host reproductive season in March (Figure 25). Fat storage in both sexes rose slightly after the first

Figure 25. Seasonal changes in mean fat index values of all Gambusia affinis (solid line) and females only (dashed line) in Tramline Pond, December, 1974 - December 1975.


MEAN FAT
4
2
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1974
1975
MONTH

wave of new births, dropped to a low value in June when the second wave of young were entering the population, and then rose to a new peak in the fall. The same pattern obtained in Alligator Bayou and Grants Bayou except that the mean index values remained low after March with no mid-spring rise as shown in Figure 25. Since many fish from Tramline Pond necropsied during April and May were large members of the overwintering population, the increase in fat storage during these months was probably due to partial recovery after release of the first spring brood. Fat storage was usually greater in adult females than in males and juveniles (Figure 25).

Since fat storage and O. chandleri worm burdens varied with size and sex of mosquitofish, as well as with season of capture, a method was devised to minimize the effects of these factors in the analysis of O. chandleri effects upon fat storage. For each sex and each monthly sample, mosquitofish were placed in two groups depending upon whether their fat index values were above or below the mean for the month in which they were captured. Once assigned to "high fat" and "low fat" groups, standard t-tests were employed to determine if there were significant differences in O. chandleri worm burdens between the two groups within each sex. The same procedure was used to detect differences in Posthodiplostomum minimum infections among "high fat" and "low fat" groups of male and female mosquitofish.

Both O. chandleri and P. minimum worm burdens were significantly higher in male and female mosquitofish which had fat index values less than the mean for the month of their capture (Table 12). These results suggest that both O. chandleri and P. minimum affect the general welfare of the host as indicated by their ability to store fat. But

Table 12. Mean infection intensities of Octospiniferoides chandleri and Posthodiplostomum minimum in male and female Gambusia affinis with high and low mesenteric fat deposition.

Parasite	Male Hosts		Female Hosts	
	High Fat	Low Fat	High Fat	Low Fat
O. chandleri	1.68	3.34*	6.41	11.36**
P. minimum	1.69	6.08**	4.66	6.53**

* significantly different at 0.05 level
** significantly different at 0.01 level

further tests indicated that there was a very highly significant correlation between O. chandleri and P. minimum infections in Tramline Pond mosquitofish. This is not surprising when one considers that the factors influencing the degree of parasitism by O. chandleri (size, sex, and age of the host, general condition of the host immune system) might be expected to influence P. minimum infections. But when this type of confounding occurs, it is impossible to determine which of the two parasites had the greatest effect upon host fat storage, or indeed, whether only one or perhaps both were required to produce the effect. It is possible that one of the parasites could be found more frequently in "low fat" hosts because of its association with the other parasite which might be the sole cause of the "low fat" condition. Although this problem would have to be resolved with experimentation under controlled laboratory conditions, it is probable that both O. chandleri and P. minimum affect fat storage in their mosquitofish host to some degree. Because of the more intimate relationship between a metacercarial trematode and its host, P. minimum might be expected to have the greater effect upon mosquitofish fat storage.

Effect upon Fecundity

The fecundity of female mosquitofish from Tramline Pond was examined before attempts were made to determine the effect of O. chandleri worm burden upon mosquitofish reproduction. Brood sizes encountered in the course of the study ranged from 1 to 37 and mean brood size was 15.3 embryos. Krumholz (1948) reported brood sizes

varying from 1 to 315 among the mosquitofish in southern Illinois. Bonham (1946) reported a mosquitofish from a Texas pond which contained 354 embryos. Fecundity in Tramline Pond is low, therefore, and very few of the studies reviewed by Krumholz (1948) reported lower maximum brood sizes. None reported lower mean brood sizes. Brood size in Tramline Pond mosquitofish increased with mother size ($r=0.61$, $P < 0.001$).

Multiple regression analysis was employed to investigate the effect of O. chandleri infections upon brood size in Tramline Pond mosquitofish. This approach allowed accounting for the effects of mother size and season which have been shown to affect brood size. The analysis showed that season had a very highly significant ($P < 0.0001$) effect upon brood size. Mother size showed a significant effect when O. chandleri was removed from the analysis ($P < 0.05$). O. chandleri seemed to have no effect at all upon brood size. The probability of a larger F value for testing the significance of the regression was 0.73.

Effect upon Host Population

There is no evidence from the information gathered during this study that O. chandleri can cause mosquitofish mortality in Tramline Pond. Large numbers of O. chandleri were found in mosquitofish alimentary tracts only in April at which time most of the worms were earliest juveniles. The effects of these worms on the host would be expected to be related to their biomass which would be similar to that of three or four large worms. Also, increases in intensity of

O. chandleri infections were nearly always accompanied by increased mortalities (compare Figure 18 to Figure 21a). This indicates the operation of density-dependent mortality suggesting that the parasites regulate their numbers at levels below those at which they could cause host mortality.

The role of O. chandleri in the regulation of mosquitofish population was not specifically pursued in this investigation, but much of the information obtained has bearing on that question. Crofton (1971a) pointed out that if parasites can and do kill their hosts, that the nature of their distribution among hosts (the negative binomial distribution) guarantees the development of stable equilibria in both parasite and host populations. In essence, he contends that an increase in host density increases the rate of host-finding success in parasites. Since parasites reproduce faster than their hosts, their densities increase at a faster rate. The negative binomial distribution of parasites dictates that a particular proportion of the hosts will have infection intensities above the lethal level and will die. The death of these heavily infected hosts imposes a higher mortality on the parasite population. Thus, both parasite and host populations decline. In a similar manner, declining host populations are bolstered by a declining parasite population and decreased parasite-induced mortality. Crofton (1971b) demonstrated the operation of this type of population control and explored the effects of negative binomial parameters, the lethality of the parasite, and parasite and host reproductive rates upon the establishment of equilibrium levels. He also applied the model convincingly to field data on Polymorphus minutus in its amphipod intermediate host to demonstrate that this

mechanism does operate in nature.

May (1977) pointed out two faults in Crofton's model: 1) conclusions were drawn from simulations based on a very restricted range of parameter values, and 2) the probability of success of the parasite transmission stage was not constrained to values less than one. May corrected these faults and determined that they changed few of Crofton's conclusions. Anderson (1978) varied pairs of parameters in a model based upon Crofton's model while keeping others constant and showed the ranges of parameters within which stability occurs in parasite and host populations. Factors contributing to stability and instability in parasite-host systems were examined by Anderson and May (1978) and May and Anderson (1978), respectively. In all four of the papers mentioned above, Crofton's lethal level (L) is replaced by the pathogenicity term (α) defined as the slope of the linear function relating host mortality and parasite burden. Other elements of these later models differ little in concept and function from Crofton's model and the basic assumptions are the same.

Crofton's basic assumption was that parasites can and do kill their hosts. This assumption has two parts; 1) for each parasite-host system, there is some infection intensity (L) that is lethal to the host and 2) these lethal infection intensities do occur in nature. The first part must be conceded because no host has an infinite capacity to support parasites. The second part of the assumption is moot.

In its ostracod host, O. chandleri probably does cause mortality under natural conditions. In the laboratory, prolonged exposure to acanthocephalan eggs or exposure to large numbers of eggs tends to

result in high ostracod mortality (Ward, 1940; Hopp, 1954). Also, multiple O. chandleri infections were common in the laboratory but were not found in natural ostracod infections. Of course this could result from the general rarity of natural infections but it might indicate mortality among ostracods with multiple infections in nature. As mentioned above, Crofton demonstrated parasite-induced intermediate host mortality in the case of Polymorphus minutus infections in amphipods.

Acanthocephalans in their intermediate hosts might be expected to have maximum effect upon that host because they are in intimate contact with its tissues. Also, except for encapsulation, killing, and assimilation of a parasite, these hosts have no way of removing them. Apparently, intermediate hosts of acanthocephalans have poorly developed immune responses. Cysts which are mostly a product of host immune response are absent in O. chandleri and other neoechinorhynchids (Ward, 1940; Harms, 1965; Dill, 1974). DiGiusti (1949) reported that the amphipod host of Leptorhynchoides thecatus could not encapsulate and destroy the larvae unless low temperature slowed the parasite growth rate. Thus, arthropod hosts have little defense against acanthocephalan parasites and tend to accumulate them. Although heavy acanthocephalan infections may result in growth retardation among the parasites (DiGiusti, 1949), the accumulation continues and may eventually kill the host.

On the other hand, acanthocephalan parasites seem to have little effect upon their definitive hosts. The observations on O. chandleri seem to indicate that the demands upon the host are small. Decreased fat deposition was the only demonstrable effect of their presence and

it is not clear whether this effect is truly due to O. chandleri infections. It is often difficult to demonstrate the effects of intestinal helminths upon their hosts. Klein, Olsen and Bowden (1969) infected trout with the intestinal fluke, Crepidostomum farionis, and then compared the length, weight, condition factor, hemoglobin, hematocrit, swimming endurance and percentage body fat of the infected fish with controls. They found significant differences only in hemoglobin and hematocrit levels.

In definitive hosts there is always an exit route for intestinal helminths that does not require host death. Worms that lose their purchase on the gut wall simply pass out with the host feces. O. chandleri in mosquitofish seem to be lost in this manner as a result of intraspecific competition. Whenever population density increased, mortality increased. Short periods of starvation also cause O. chandleri to be lost from mosquitofish (Downey and DeMont, 1978). This is a general phenomenon that has been demonstrated in other parasites of mosquitofish (Davis and Huffman, 1975), intestinal helminths of marine fishes (Möller, 1976), tapeworms in chickens (Reid and Ackert, 1941; Reid, 1942), and acanthocephalans in rats (Burlingame and Chandler, 1941). Acanthocephalans can be steadily lost from their hosts whether there is stress or not. This is obvious by the constant mortality exhibited at every age by O. chandleri (Figures 23 and 24). Neoechinorhynchus cylindratus, too, was lost continuously from a largemouth bass fed infective bluegills (Ward, 1940). These observations agree well with the idea that each acanthocephalan population is in dynamic equilibrium balanced by constant gain and loss of individuals as proposed by Chubb, Awachie and

Kennedy (1964).

Crofton's model requires that as the parasite population increases, truncation occurs in the tail of its negative binomial distribution due to the mortality of heavily infected hosts. There is no evidence that this occurs in the O. chandleri - mosquitofish system. O. chandleri distribution in Tramline Pond mosquitofish fit the negative binomial distribution in both the cold months (October-March) and the warm months (April-September) ($P < 0.05$). Mean intensity of infections was higher (8.8 worms/host) in the summer months than in the winter months (6.3 worms/host). Over dispersion in the summer population was greater as indicated by the ratio of the variance to the mean (29.0 as opposed to 5.7 for the winter months). Despite these differences in distributional parameters, there was no significant difference between the form of the two negative binomial distributions when they were tested using the Kolmogorov-Smirnov two-sample test ($P < 0.05$) (Siegel, 1956). The differences in mean intensity and variance were apparently due to a few high intensity infections which occurred during the summer months and were due entirely to large numbers of very small worms. High intensity infections should not occur if host mortality is parasite induced.

It seems very unlikely that a parasite so sensitive to its own population pressures and more sensitive than the host to stresses such as short fasts could become abundant enough to kill its host. It seems reasonable to conclude that the second part of Crofton's basic assumption is not satisfied in the case of O. chandleri in its definitive host and the kind of population control mechanism that he outlined cannot operate in this system. This conclusion may be supported by

the negative binomial parameters estimated in this study. Assuming that the pathogenicity (α) of O. chandleri if not zero is at least very small, these distributional parameters tend to fall outside of the ranges of values in which regulation of the host population is possible (Anderson, 1978).

It is interesting to speculate that the acanthocephalan parasites may actually help their definitive hosts in various ways. Consider, for instance, the idea that the parasite pays a "dowry" when, by altering the intermediate host's behavior, it presents the definitive host with a meal for a very small energy investment. Of course the energy content of one ostracod, in the case of O. chandleri, would not go far toward paying for a lifetime of support from the host. But consider the dynamics of the situation. Very many worms fail to become established after making their "payment" and others suffer a high and constant mortality. Very few of the potential recruits live to full maturity and the average lifespan is probably quite short. Under these circumstances it is feasible that the host receives more than it gives. This could be especially true if the parasite's "payment" is received in winter or early spring when energy might be in short supply and in high demand and payed back in support to the worm two or three months later when food may be abundant and energy cheap.

Acanthocephalans could supply metabolites to the host during periods of low food availability. Von Brand (1966) suggested that acanthocephalans store so much glycogen that they could act as storage tissue for their host. Read and Rothman (1958) reported that when rat hosts were starved for 48 hours, Moniliformis dubius glycogen levels fell to 12% of their original value. At least one of the

metabolic by-products of acanthocephalan metabolism, ethanol, could be easily absorbed and used by the host. Similarly, acanthocephalans could help their host by failing before the host in times of critical food shortage so that the host does not have to share what little food there is available.

In a broader sense, acanthocephalans and other helminth parasites may aid their host by contributing to the stability of the community to which the host belongs. Increasing the number of freeliving species in an animal community increases the complexity because of the additional possible trophic interactions. As the complexity increases, community stability is believed to be enhanced as each species becomes less dependent upon one or a few other species.

Additional complexity is added when parasitic animals are considered. Increasing numbers of freeliving animals provide opportunity for the establishment of parasites that require several hosts to complete their life cycles. These parasites contribute to the community complexity through increased direct (trophic) interactions or through indirect interactions deriving from the complex nature of the parasite life cycles. These indirect interactions add a whole new dimension to the complexity of animal communities.

Helminth parasites can increase community stability by creating trophic links in the food web. In the case of O. chandleri, its effect on the behavior of the ostracod host makes them susceptable to predation by young bluegill as well as mosquitofish. The bluegill is not a suitable host for O. chandleri and benefits from an easy meal without becoming infected. The parasite thus improves the efficiency of energy transfer in a part of the trophic web outside of its life

cycle. Moreover, since the bluegill does not usually utilize the benthic ostracods to a great extent, a new trophic link is created to enhance community complexity and stability.

Parasites may be a factor in defining roles in competitive interactions between freeliving animals. When two animals occupy very similar niches, they are exposed to the same infective stages of parasites. The problem of susceptibility to the various parasites then becomes a factor in determining which of the two competing species will have a competitive edge.

Although parasites increase complexity in animal communities, some may also tend to break down niche partitioning and force competition. Crowden (1976) reported that dace parasitized by the eye worm, Diplostomum spathaceum, grew as fast and maintained their condition as well as uninfected individuals. Infected fish, however, were less efficient predators and had to extend their feeding periods much later into the evening to obtain enough food. This very likely placed them in competition with some nocturnal feeders. The infected dace also spent more time in the surface layers of the water competing with surface feeders. Similarly, ostracods infected with O. chandleri undoubtedly compete with other microcrustaceans for food in the surface layers. Parasites may also interfere with niche partitioning when the size of food taken is an important factor. Pearre (1976) found that hemiurid trematode infections caused gigantism in chaetognaths which resulted in a dietary shift towards larger prey organisms.

Parasites may also constitute a form of communication between seemingly isolated communities or ecosystems. In Tramline Pond, this can be illustrated by the parasites which use mosquitofish as inter-

mediate hosts and develop to maturity in fish-eating birds. Since the birds, regularly visit many ponds in the area which are otherwise isolated, their parasitic worm burden represents the "average" availability of infective stages in all of the ponds which they visit. Under these conditions, the ponds which have the least favorable conditions for development of mosquitofish infections tend to dilute the effect that favorable ponds have upon the worm population in the birds. This means that the favorable ponds get back less than their fair share of parasites from the bird (worm eggs in bird feces) and the unfavorable ponds receive more than their share. Thus weak parasite populations in the ponds may tend to be bolstered and strong populations may tend to be restrained. Most importantly, the controls on the parasite populations and the concomitant effects upon other organisms in each pond system have their origin in another, seemingly remote system.

Summary of O. chandleri Effects

In summary, helminth parasites like O. chandleri can and do kill their intermediate hosts and are likely to function in the population control of those hosts in the manner described by Crofton (1971b). O. chandleri, and probably many other intestinal helminths, have minimal effects upon their definitive hosts and seem to control their own numbers through density-dependent mortality in a manner similar to many free living organisms. Similar conclusions were reached by Grundman, Warrock and Wassom (1976). Although control of definitive host numbers by Crofton's mechanism is very unlikely, intestinal helminths may interact with the host in some other ways, some of which may be beneficial to the host.

SUMMARY AND CONCLUSIONS

Life Cycle

Octospiniferoides chandleri has a typical neoechinorhynchid life cycle using the ostracods Physocypria pustulosa (Sharpe 1898) and Cypridopsis vidua (Müller 1776) as intermediate hosts. Development to the cystacanth stage in the ostracod takes 20 days at 23 C and 23 day-old cystacanths are infective to Gambusia affinis. The alteration of ostracod intermediate host behavior by an acanthocephalan parasite is reported for the first time. Male development in the definitive host is gradual with no distinct stages. Female development is divisible into four easily recognized stages. Growth rates in the definitive host are linear with females growing faster than males. Temperature is inversly related to the duration of the earliest female stage. This study brings the number of known neoechinorhynchid life cycles to nine.

Spatial Distributions

Well-established populations of O. chandleri occur in lentic habitats in south Louisiana where its major host, Gambusia affinis, and ostracods are abundant. Interspecific competition occurs between O. chandleri and Homalometron armatum (reported here for the first time from mosquitofish), but the nature of the competition does not affect O. chandleri distribution. O. chandleri in Tramline Pond are distributed among the mosquitofish hosts according to the negative binomial distribution and are more prevalent in females and larger fish. Within

individual hosts, they show site preference which varies with parasite size (age) and sex.

Temporal Distributions

Traditional interpretations of the seasonal changes in the Tramline Pond O. chandleri population are confusing and indicate two or three periods of recruitment. Calculating recruitment using the rate of acquisition of young females and the temperature-adjusted duration of this stage indicates that most recruitment takes place during the warm months of the year. Mortality rates tend to balance recruitment. The traditional interpretation of acanthocephalan seasonality showing maximum recruitment in the fall and winter is shown to be in error due to the failure to consider the effects of temperature on the development of the worms. O. chandleri seasonal patterns meshed well with host seasonality.

Effects upon the Host

No mosquitofish pathology can be attributed to O. chandleri infections and infections have no effect upon definitive host fecundity. O. chandleri might have an effect upon fat storage in mosquitofish. There is no evidence to suggest that O. chandleri functions in the control of mosquitofish populations but the larval parasites may influence ostracod populations through the mechanism described by Crofton (1971b).

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VITA

David Joseph DeMont was born in Auburn, New York on December 7, 1938. He attended public schools and graduate from Port Byron Central High School in June 1957. After spending four years as a U.S. Navy electronics technician, he attended college in New York and California. He earned a B.A. degree in Biological Science from San Jose State College in January 1967 and a M.S. degree in Fisheries Science from Humboldt State College in December 1971. He worked for two years as a Research Fisheries Biologist for the North Carolina Natural Resources Commission before joining the staff of the LSU Department of Forestry and Wildlife Management as a Research Associate. Mr. DeMont is currently a candidate for the Doctor of Philosophy degree in Marine Sciences at Louisiana State University.

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EXAMINATION AND THESIS REPORT

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Major Field: Marine Sciences

Title of Thesis: THE LIFE CYCLE AND ECOLOGY OF Octospiniferoides chandleri BULLOCK 1957 (ACANTHOCEPHALA)

Approved:

C. F. Bryan
Major Professor and Chairman

Carolyn H. Hargrave
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Date of Examination:

September 25, 1978